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AMERICAN MALACOLOGICAL BULLETIN

VOLUME 10 NUMBER 1

Biannual Journal of the American Malacological Union

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Histology and cell ultrastructure of the mantle and mantle lobes of the Eastern oyster, *Crassostrea virginica* (Gmelin): a summary atlas

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Abstract. The mantle and mantle lobes of *Crassostrea virginica* are described using light and scanning and transmission electron microscopy. Also, literature on these structures in bivalves is reviewed.

Two types of goblet shaped secretory cells are found in the epithelium surrounding both the mantle and its lobes. There are tracts of ciliated epithelial cells on the inner or pallial surface of the mantle, and on the inner and middle lobes; whereas the outer or shell surface, and the outer lobe have few ciliated cells. Ciliated single celled receptors are present at the distal ends of the tentacles, and probably also on the pallial surface of the mantle. Many of the epithelial cells of the shell surface have extensive basal invaginations, as often found in cells associated with ion transport. The muscle fibres and associated glial cells of the mantle and its lobes have a similar appearance to those of adductor muscles, except that intermuscular junctions are common. The diameters of the thick myofilaments of the radial muscle of the mantle are similar to those of the opaque part of the adductor muscle, whereas the thick myofilaments of the subepithelial muscle fibres and the muscle fibres in the lobes are thinner.

The periostracal gland consists of flattened epithelial cells at the base of the periostracal groove, that have extensive apical processes surrounded by periostracum. The latter forms a thin sheet that extends out over the inner surface of the outer lobe, that is covered with secretory granules. This surface is composed of epithelial cells surrounding crypts, and goblet cells full of secretory granules, often with cell bodies extending below the epithelium.

The mantle of bivalves is important in the transport of materials for addition and removal of material to the shell (Neff, 1972b; Wilbur, 1972, 1985; Machin, 1977; Crenshaw, 1980), and as a source of nutritional reserves. Mucous secretions protect the permeable integuement, and ciliary movement moves the mucus and attached particles to the periphery (Galtsoff, 1964; Machin, 1977). The mantle lobes at the distal edge are important in periostracum and shell formation (Beedham, 1958; Neff, 1972a, b; Bubel, 1973a; Saleuddin and Petit, 1983) and detection of stimuli (Moir, 1977).

The general anatomy and histology of the mantle and mantle lobes have been described by Galtsoff (1964) using light microscopy, but the features are demonstrated only with drawings. The purpose of this study is to provide a preliminary survey of the histology and cell ultrastucture of the mantle and its lobes, using light micrographs of thin resin sections as well as transmission and scanning electron microscopy. The study is limited to the region of the mantle extending from the adductor muscle to the distal edge, opposite to the hinge.

METHODS OF PREPARATION

Two mature oysters that were maintained in ambient seawater at about 4ºC were fixed for light (LM) and transmission electron microscopy (TEM). One of these specimens was relaxed before fixation by placing it in seawater containing 8% magnesium sulphate (Galtsoff, 1964) in a refrigerator at about 4ºC. Relaxation took approximately 1.5 hours. Two oysters which were used for preparation for scanning electron microscopy (SEM) were maintained in seawater at 20ºC. One of these was fixed after relaxation with 8% magnesium sulphate at 20ºC, which took about 6 hours.

The four oysters used in this study were opened by cutting through the adductor muscle. For LM and TEM, pieces of mantle from each oyster extending from the adductor muscle to the distal edge in the region opposite to the hinge (Fig. 1: area A) were excised and pinned out on dental wax. One sample from each oyster was placed in Karnovsky's fixative in phosphate buffer (Karnovsky, 1965), and another was placed in 1G4F (McDowell, 1978) with seawater replacing some of the buffer solution (Howard and Smith, 1983). For SEM, one piece of mantle was excised from each animal as for LM and TEM, but was not pinned to a surface, since the surface details of the shell or outer surface were also needed for study. Another sample of mantle was removed attached to the shell, by sawing through both the mantle and shell with a jeweller's saw. All SEM samples were fixed in 1G4F with seawater. After fixation overnight, the tissues for LM and TEM were cut into strips oriented in the axis from the proximal to the distal edge of the mantle (LS), or across this axis (TS). The samples for LM included the lobes, whereas the samples for TEM were cut into smaller pieces, and the edge of the mantle with the lobes was separate. Samples for SEM

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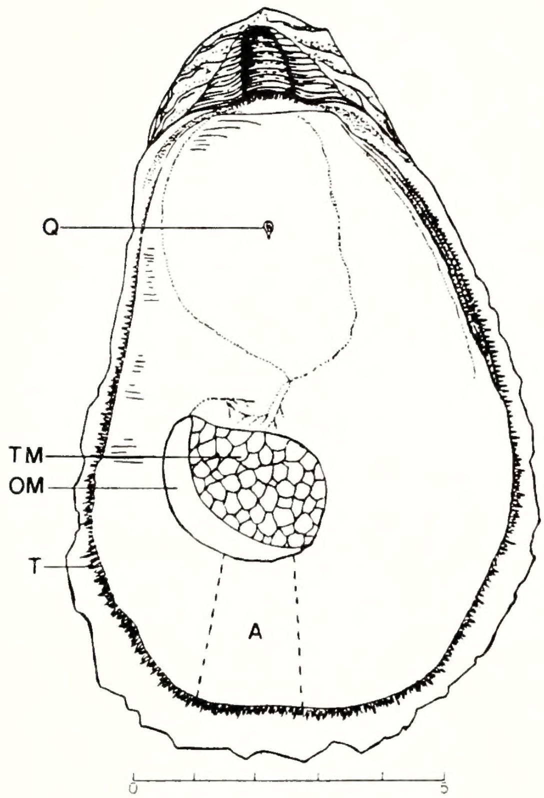


Fig. 1. Oyster viewed from right side, with right valve removed (redrawn from Galtsoff, 1964).

were kept whole. All fixatives and buffers for light and electron microscopy were at pH 7.2.

Samples for LM were dehydrated in methanol and embedded in JB4 resin. For TEM, samples were post-fixed in 1% osmium tetroxide, dehydrated in acetone then embedded in Taab resin (Marivac Ltd., Halifax, N.S.). LM and TEM samples were embedded so that they would be sectioned in LS or TS. Some LM samples were also embedded so that they would be sectioned parallel to the surface of the mantle. The LM sections were stained with a 1:50 dilution of 1% toluidine blue in 1% sodium borate, or Van Gieson stain (Dougherty, 1981). Taab resin semi-thin sections for light microscopy were also stained with toluidine blue. Sections for TEM were stained with 25% uranyl acetate in methanol (Stempack and Ward, 1964) and lead citrate (Reynolds, 1963), and viewed in an Hitachi HS 9 transmission electron microscope.

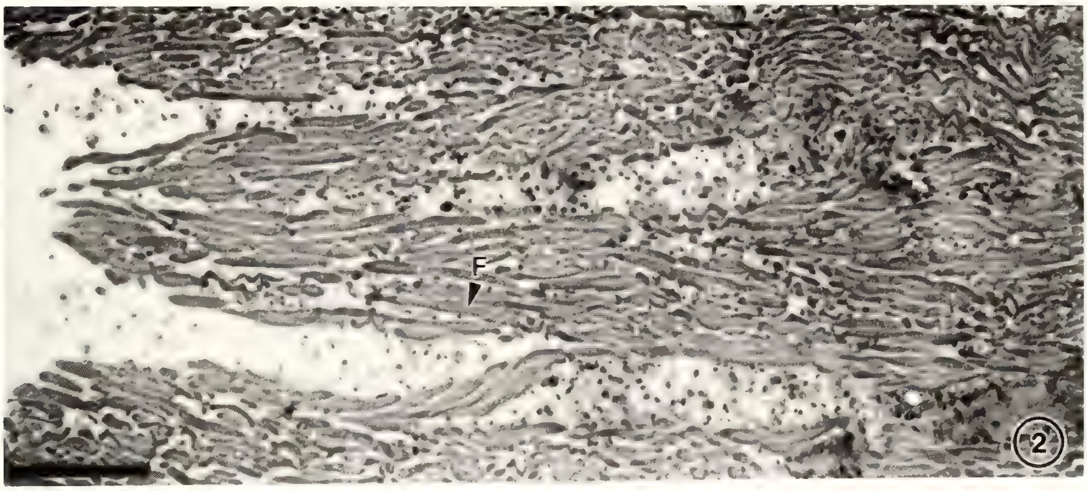
TEM negatives of transverse sections of the muscles of the mantle and lobes were magnified X10 using a Nikon profile projector, and diameters of the thick myofilaments were measured using the micrometers on the projector. SEM samples were post-fixed in 1.5% osmium tetroxide, dehydrated in acetone, critical-point dried, mounted with either the mantle surface facing the pallial cavity or facing the shell uppermost, and sputter-coated with gold. They were viewed in an Hitachi S-2400 scanning electron microscope.

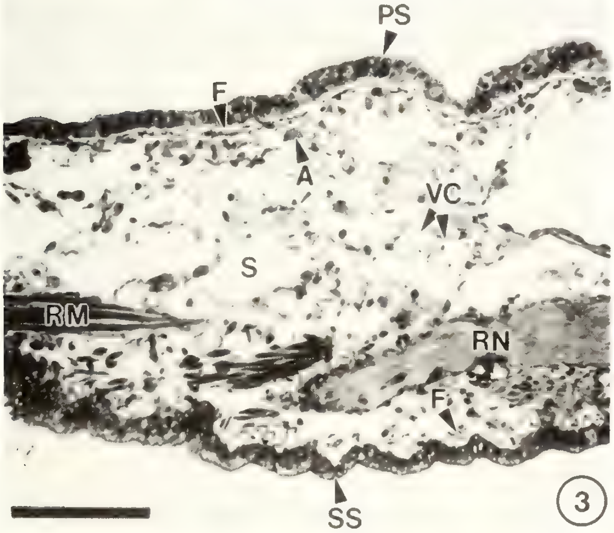
The following abbreviations are used in the plate captions and elsewhere in this paper (specimen preparation): K,-Karnovsky's fixative: 1% glutaraldehyde-4% formaldehyde (from paraformaldehyde); 1G4F,-1% glutaraldehyde -4% commercial formaldehyde in phosphate buffer with sea-water added; MS,-specimen relaxed in magnesium sulphate; JB4,-specimen embedded in JB4 for light microscopy; 0.5μm,-0.5μm. section of specimen embedded for electron microscopy, stained with toluidine blue; CMB,-chromotrope 2R-methylene blue; MBBF,-methylene blue-basic fuschin; TB,-toluidine blue; VG,-Van Gieson; L.S., longitudinal section; T.S., transverse section; (cell structure): A,-amoebocyte; AX,-nerve axon; BM,-basement membrane; C,-cilia; CA,-circumpallial artery; CE,-cytoplasmic extension; CF,-collagen fibres; CL,-cross-links; CM,-circular muscle; CN,-circumpallial nerve; CR,-crypt; DB,-dense body; DBA,-diagonal banding; EC,-endothelial cell; F,-muscle fibre; G,-granule; GA,-Golgi apparatus; GC,-glial cell; GL,-glycogen; HD,-hemidesmosome; J,-junction; L,-lipid droplet; M,-mucus; MC,-mucous cell; MI,-mitochondrion; ML,-middle lobe; MV,-microvilli; N,-nucleus; NE,-neuromuscular ending; OM,-opaque portion of adductor muscle; P,-periostracum; PC,-pallial curtain; PG,-periostracal groove; PGI,-periostracal gland; PS,-surface of mantle proximal to pallial cavity (pallial surface); rudimentary Quenstedt's muscle; RC,-receptor cell; RER,-rough endoplasmic reticulum; RM,-radial muscle; RN,-radial nerve; S,-sinusoid; SC,-secretory cell; SER,-smooth endoplasmic reticulum; SG,-secretory granule; SGC,-secretory granular cell; SL,-shell lobe; SM,-secretory material; SP,-spicule; SR,-sarcoplasmic reticulum; SS,-surface of mantle proximal to shell (shell surface); T,-tentacle; TBA,-transverse banding; TM,-translucent portion of adductor muscle; TNM,-thin myofilaments; TKM,-thick myofilaments; V,-vesicle; VC,-vesicular cell; VG,-vesicle with irregular, electron-dense, granular contents.

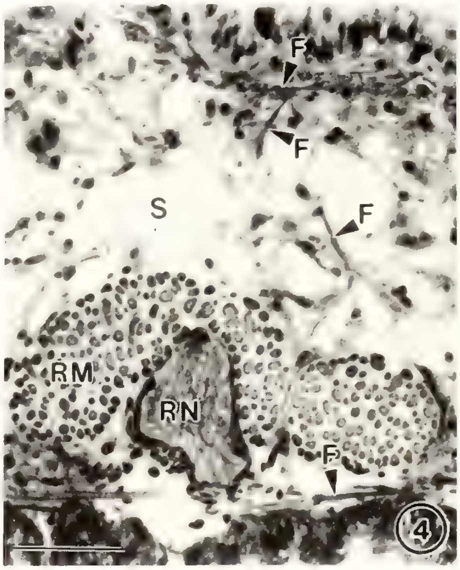
RESULTS

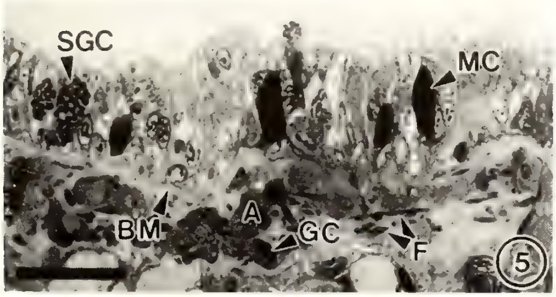
A conspicuous feature of the mantle is the fan-like arrangement of the radial muscle, which can be seen in a section cut parallel to the surface (Fig. 2). This results in more muscle being present peripherally in the mantle. The radial muscle and accompanying nerves are near the surface proximal to the shell, and sometimes the nerves are surrounded by muscle fibres (Figs. 3, 4). The mantle consists of a spongy network of vesicular cells, separated by blood vessels and sinusoids, and is covered by a columnar epithelium. Often there are amoebocytes between the vesicular or epithelial cells. Small muscle fibres occur beneath the epithelium, and also run across the tissues of the mantle.

Most of the epithelial cells on the inner or pallial sur-









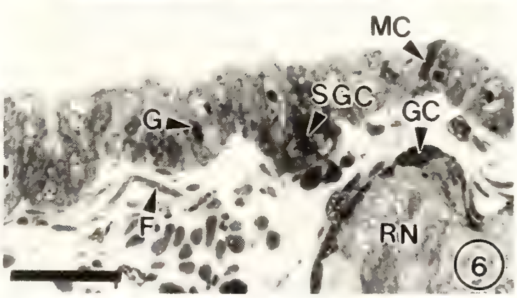


Fig. 2. The section is cut parallel to the surface of the mantle. The muscle fibres of the radial muscle radiate out from the region where the mantle is attached to the body, at the left, to the outer edge of mantle, at the right (IG4F, MS, JB4, CMB, scale bar = 0.1 mm). **Fig. 3.** L.S. mantle. A columnar epithelium covers the upper, pallial surface and the lower, shell surface. The radial nerve and the large fibres of the radial muscle are near the shell surface. There is a layer of small subepithelial muscle fibres near the shell and pallial surfaces of the mantle. Amoebocytes, large vesicular cells and sinusoids are present throughout the mantle (K, MS, JB4, TB, scale bar = 0.1 mm). **Fig. 4.** T. S. mantle. The radial nerve is surrounded by fibres of the radial muscle. Subepithelial muscle fibres are present, and muscle fibres also extend across the mantle (K, MS, JB4, CMB, scale bar = 20 μm). **Fig. 5.** Epithelium on PS of mantle. T.S. Goblet shaped secretory cells with distinct granules, one secreting its contents and mucous cells are present among columnar epithelial cells, which have microvilli and sometimes also cilia at the apex. A thick basement membrane supports the epithelium. Subepithelial muscle fibres, amoebocytes and glial cells are present below the epithelium (0.5 μm, K, MS, scale bar = 20 μm). **Fig. 6.** Epithelium on SS of mantle. T.S. The cells are columnar to cuboidal, and many contain darkly staining granules of varying shape and size. Granular secretory cells and mucous cells are present. There are subepithelial muscle fibres, and a radial nerve surrounded by glial cells (0.5 μm, K, MS, scale bar = 20 μm).

face are columnar, and a thick basement membrane is present (Fig. 5). These cells have microvilli, but there are tracts of cells which also have cilia (Figs. 5, 7 and 8). Some of the latter have several cilia interspersed with microvilli, whereas others have only one or two cilia. The narrow openings of goblet shaped secretory cells can sometimes be seen (Fig. 8). Most of the epithelial cells of the outer or shell surface are shorter than those on the pallial surface, dark granules can often be seen in them, and their basement membrane is thin (Fig. 6). These cells are usually covered with microvilli, although there are a few ciliated cells (Fig. 9). There are granules and sheets of mucus on the shell surface, and many small spicules in grooves or depressions (Figs. 9, 10).

There are two types of goblet shaped secretory cells in the mantle epithelium (Figs. 5, 6). One contains distinct, darkly staining granules (SGC), the other granules which are more closely packed and tend to coalesce, giving the appearance of a typical mucous cell (MC). The granules of the first type of cell are still distinct when they are discharged. Below the epithelia small muscle fibres run in all directions in close association with elongate glial cells containing dark, round granules. Glial cells also surround the radial nerve (Fig. 6), and accompany the radial muscle fibres (Fig. 11). In a specimen which had not been relaxed with magnesium sulphate, the radial muscle contracted and the epithelium was thrown into folds (Figs. 12, 13). On the shell surface of this specimen, there are subepithelial muscle fibres within the folds (Fig. 13).

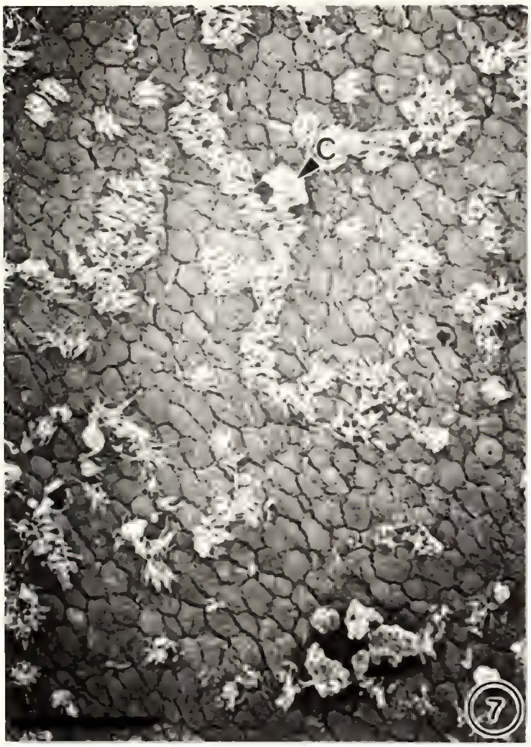
The ciliated cells of the pallial surface usually have several cilia interspersed with microvilli at the surface (Fig. 14), whereas occasionally a cell was seen with only a few cilia and microvilli at the surface (Fig. 14, insert). The nuclei of the epithelial cells are basal, but many cells do not appear to reach the basement membrane, so appear to form a partially stratified epithelium. Mitochondria are situated near the nucleus as well as in the apical cytoplasm, which also contains vesicles, some with dark-staining contents. There is a Golgi apparatus just above the nucleus, and the cytoplasm contains glycogen. In the goblet cells that contain distinct granules, mitochondria can be seen between the granules. The thick basement membrane consists of several fine, filamentous layers. The subepithelial muscle fibres are accompanied by glial cells and nerve axons.

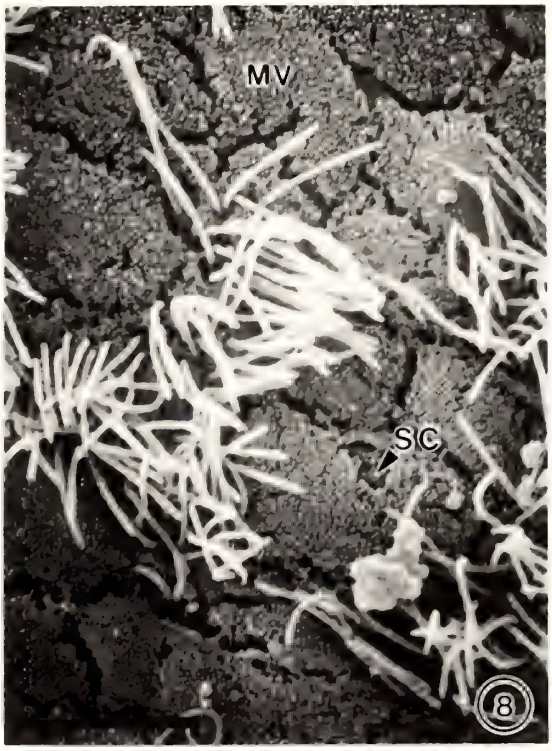
At the shell surface, the epithelial cells often have basal invaginations that form cisternae of smooth endoplasmic reticulum (Fig. 15). The latter are sometimes dilated with dark material (Fig. 15, insert). Between these invaginations are cisternae of rough endoplasmic reticulum, which also extend around the nucleus (Fig. 16). The cytoplasm contains glycogen; round granules which are not membrane-bound, and have the amorphous appearance typical of lipid; and membrane-bound vesicles containing granules with irregular shapes and of varying density that could be secondary lysosomes or phagosomes. Some cells have a darker cytoplasm, containing more densely packed glycogen, than others. Secretory cells containing the membrane-bound granules typical of mucous cells are present (Fig. 15; MC). The membranes are often incomplete where the granules are beginning to coalesce. There are also cells containing distinct, membrane-bound granules (Fig. 16: SG). Below the epithelium is a thin basement membrane.

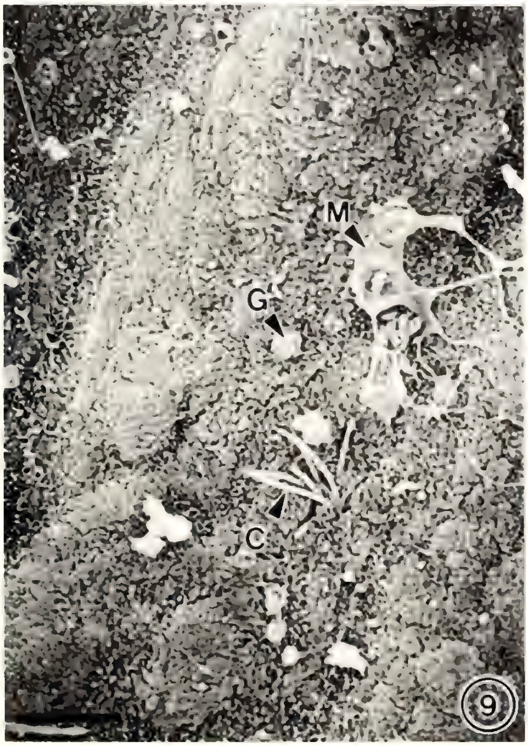
The subepithelial muscle fibres consist of a central myofibril containing thick and thin myofilaments (Fig. 17). Of 98 myofilaments measured near the pallial surface, the widest myofilament was 65 nm in diameter but most were 36-45 nm in diameter. The mean and median width was 42 nm. There are dense bodies in the centre of the myofibril as well as at the sarcolemma, where they form hemidesmosomes or attachment plaques. These muscle fibres are often closely associated with each other, and sometimes form junctions (Fig. 18). The nucleus of the muscle fibre is situated to one side of the myofilaments (Fig. 19).

The radial muscle consists of a group of muscle fibres that are larger than those beneath the epithelia (Fig. 20). Some of the fibres that are elongate in transverse section are up to 4.5 μm in diameter along the long axis, but most are about 1.4-2.9 μm in diameter. Glial cells and sometimes small blood vessels are found between the muscle fibres. There are profiles of sarcoplasmic reticulum beneath the sarcolemma, and several dense bodies can be seen at the periphery of each fibre, forming hemidesmosomes, as well as in the centre (Fig. 21). Like the muscle fibres beneath the epithelia, these fibres sometimes form junctions with each other, and with nerve-endings and glial cells. Glycogen rosettes, as well as large dense membrane-bound granules, the gliosomes, can be seen in the glial cells. The nerve-endings are usually accompanied by a glial cell, and sometimes contain small clear vesicles about 70 nm in diameter (Fig. 22), sometimes larger electron-dense vesicles about 160 nm in diameter (Fig. 23). Some endings have a mixed population of clear and dense-cored vesicles. The intercellular cleft is narrow, and does not appear to contain collagen or a basement lamina in figure 22, although there appears to be a lamina in figure 23. The nucleus of the muscle fibre is often situated in a peripheral extension of the cytoplasm, which also contains other cell organelles, such as the Golgi apparatus and mitochondria (Fig. 24). The thick myofilaments are cross-striated, and sometimes show diagonal banding like that of the adductor muscles (Fig. 25). Of a hundred thick myofilaments measured, the maximum width was found to be 109 nm, and the mode was in the category of widths of 50-56 nm. The mean width was 62 nm, and the median width 58 nm (Fig. 26). The radial nerve contains a large mass of unmyelinated nerve-cell processes surrounded by a layer of glial cells (Fig. 27).

The connective tissue of the mantle is composed of







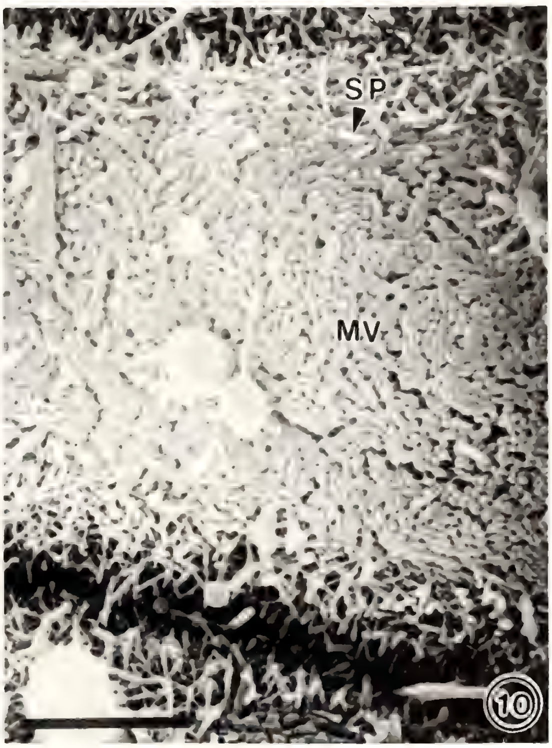
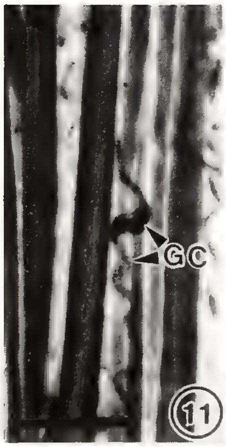
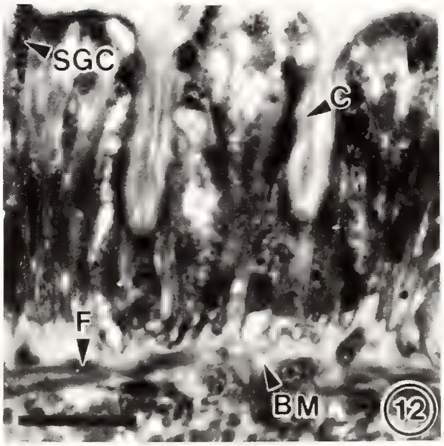
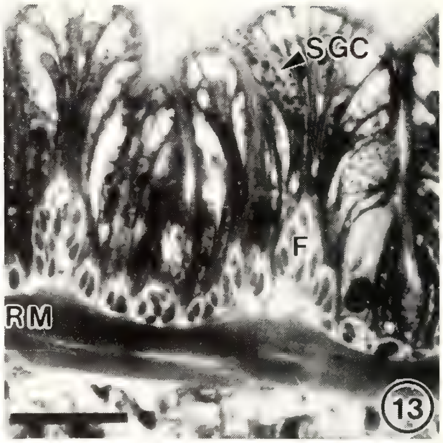


Fig. 7. Surface of PS. Most of the epithelial cells have microvilli at the apex. Tracts of ciliated cells and some cells with only one or two cilia are also present (IG4F, SEM, scale bar = 25 μm). **Fig. 8.** Surface of PS. Most of the ciliated cells have several cilia interspersed with microvilli, but some have only one or two cilia. The unciliated cells have microvilli of a constant length and width at the apex, and the openings of secretory cells can sometimes be seen between them (IG4F, SEM, scale bar = 5 μm). **Fig. 9.** Surface of SS. Most of the surface is devoid of cilia, although occasional ciliated cells are present. There is mucus and granular material on the surface of the cells (IG4F, SEM, scale bar = 5 μm). **Fig. 10.** Surface of SS. Microvilli are sometimes evident, but often they are covered by mucus, granules or spicules, especially in crevices (IG4F, SEM, scale bar = *2.5* μm).







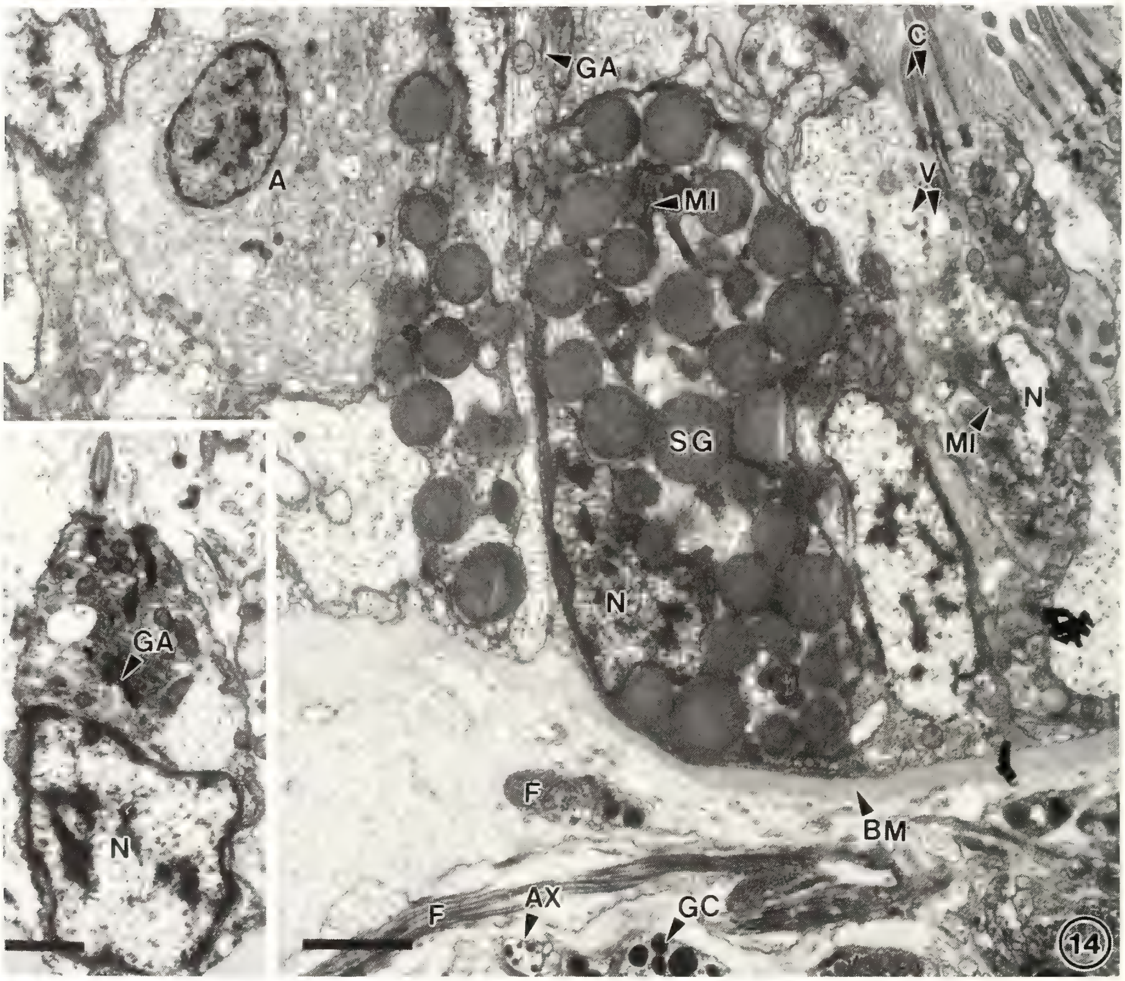


Fig. 11. L.S. radial muscle. The muscle fibres are accompanied by long glial cells containing dark granules (K, MS, JB4, VG, scale bar = 20 μm). **Fig. 12.** PS of mantle. L.S. The epithelial surface, which is supported by a thick basement membrane, is extensively folded. Small subepithelial muscle fibres are present (IG4F, JB4, TB, scale bar = 20 μm). **Fig. 13.** SS of mantle. L.S. This is from the same section shown in figure 12. Small subepithelial muscle fibres are seen in cross-section in folds of the epithelium, and thicker radial muscle fibres are seen in longitudinal section (IG4F, JB4, TB, scale bar = 20 μm). **Fig. 14.** PS of mantle. L.S. A nucleus can be seen at the base of a columnar epithelial cell with microvilli and cilia at its apex. Mitochondria surround the nucleus and are present in the apical cytoplasm, along with vesicles. Secretory cells contain discrete, darkly staining granules, and there is an amoebocyte between the epithelial cells. There are subepithelial muscle fibres, glial cells, and axons beneath the thick basement membrane (K, MS, TEM, scale bar = 2 μm). **Fig. 14: insert.** This cell, from the same area as figure 14, has a cilium and a few microvilli at the apex, mitochondria, and vesicles in the apical cytoplasm and a Golgi apparatus above the nucleus (scale bar = 1 μm).

cells with many vesicles in the cytoplasm; cells which appear to have amorphous contents, with the cell organelles pushed to the periphery; and cells containing lipid droplets with varying osmiophilia (Fig. 28). With electron microscopy, glycogen can be identified between the vesicles, and some of the cells with amorphous contents are also filled with glycogen (Fig. 29). An electron micrograph of part of a vesicular cell containing lipid droplets of low osmiophilia is shown in Fig. 20, where it occurs among the radial muscle fibres. Numerous small muscle fibres form a network in the mantle, forming junctions with each other. They are similar to those found beneath the epithelium, and consist of a central bundle of myofilaments, with the nucleus and other cell organelles in a peripheral extension of cytoplasm. Glial cells are also present.

As in most bivalves, the outer border of the mantle is divided into three lobes (Fig. 30; Galtsoff, 1964). The radial muscle is thicker at the outer edge of the mantle, so that it extends to the pallial surface (Figs. 30, 31). A band of circular muscle is also seen near the pallial surface at the base of the lobes (Figs. 30, 31). In this region many goblet shaped secretory cells of both types are present in the shell and pallial epithelia, and the bases of these cells often extend below the shell epithelium (Fig. 31).

The outer or shell lobe, which secretes the periostracum, does not have tentacles; the middle lobe is sensory, and has long, stout tentacles separated from each other by several short, slender tentacles. The inner lobe or pallial curtain is muscular, and can be extended into the mantle cavity (Fig. 33), so that the long, stout tentacles of the apposing inner lobes interlock (Galtsoff, 1964).

Most of the epithelium covering the lobes is columnar, similar to that covering the rest of the mantle (Figs. 34, 35). Many goblet shaped secretory cells are present on the outer (facing the shell) surface near the base of the inner lobe, and on the inner (facing the pallial cavity) surface of the middle and outer lobes. The bodies of the cells on the outer lobe often extend below the epithelium. The epithelial cells in the base of the groove between the inner and middle lobes are more or less cuboidal. The circumpallial nerve is proximal to the base of this groove. The flattened secretory cells of the periostracal gland are at the base of the groove between the outer and middle lobes. Fibres of the radial muscle extend into the lobes, and muscle fibres also run in various directions within each lobe.

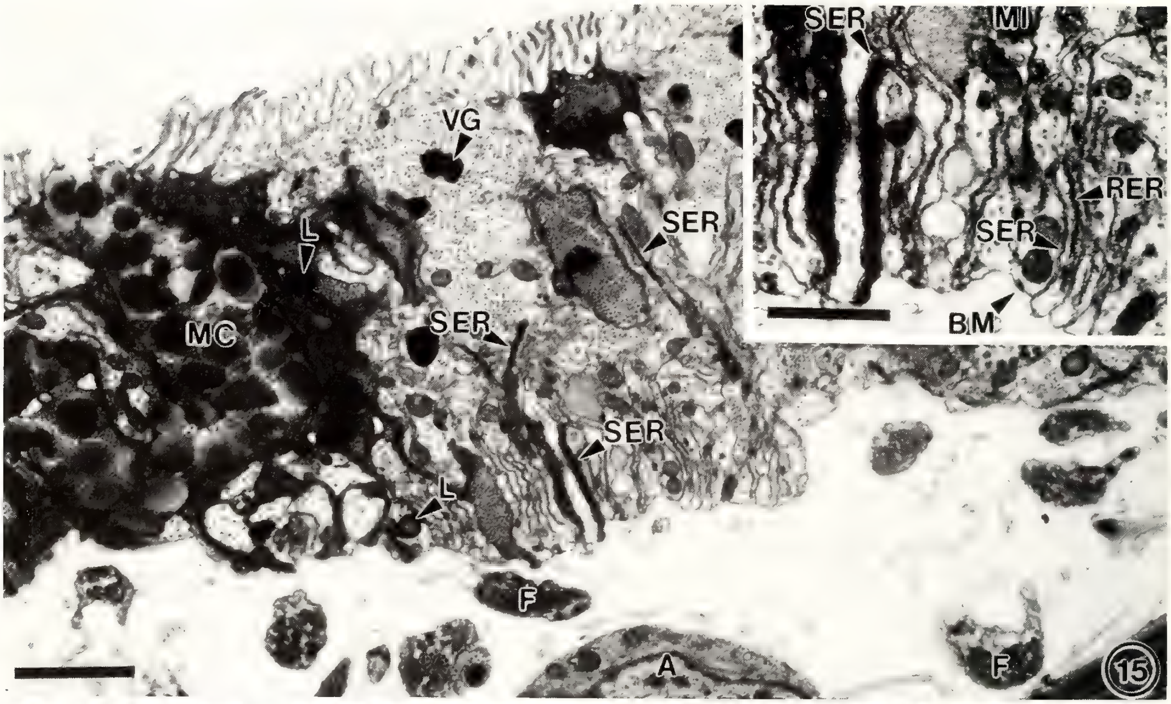
The epithelial cells of the inner surface of the inner lobe have cilia as well as microvilli (Figs. 36, 37). These cells also have several elements of Golgi apparatus as well as vesicles, some closely associated with the Golgi apparatus, and many mitochondria in the apical cytoplasm (Fig. 37). The epithelial cells of the outer surface contain similar organelles but are less heavily cilated, and have larger vesicles in the apical cytoplasm, some of which are darkly staining (Fig. 38). The epithelial cells on both surfaces have well developed apical junctional complexes, and the adjoining plasmalemmas are very convoluted. There are longitudinally oriented subepithelial muscle fibres below both surfaces.

In the centre of the lobe there are groups of cells similar to the vesicular cells of the mantle, containing glycogen, vesicles and occasionally lipid droplets, as well as muscle fibres oriented in all directions (Fig. 39). There are thick and thin myofilaments and dense bodies in the myofibrils of the muscle fibres, and junctions are sometimes present between them (Fig. 40). Occasionally the dense bodies show oblique orientation for short distances. Out of 47 measurements of the diameters of the thick myofilaments of the muscle fibres from the inner lobe, the widest diameter was 63 nm, the mean and median widths were 48 nm, and the mode was 45-54 nm.

The middle lobe has many goblet shaped secretory cells on its inner epithelial surface and distinct granules can be distinguished in most of them (Figs. 41, 42). The apical cytoplasm of the epithelial cells, some of which are ciliated, is packed with vesicles (Fig. 42). The ciliated cells are in small groups, with the exception of the outer border between the tentacles, which is more heavily ciliated (Figs. 43, 44). This is in contrast to the heavily ciliated inner surface of the inner lobe (Figs. 43, 45). The tentacles of the middle lobe are covered by small tufts of cilia, except near the tip, which is more heavily ciliated (Fig. 46). Besides cells with many cilia, there are some with only one or a few shorter cilia, which often face in different directions (Fig. 47). On the tentacles of both the middle and inner lobes some ciliated cells with darkly staining cytoplasm extend below the epithelial surface, connecting with structures that are apparently nerves (Fig. 48).

There are few goblet shaped secretory cells on the heavily ciliated outer surface of the middle lobe (Figs. 41, 49), which is covered by a layer of secretory material (Fig. 49). There are many vesicles and sometimes small dense granules in the apical cytoplasm of the epithelial cells, and sometimes blebs of apical cytoplasm containing vesicles appear to join the secretory material on the epithelial surface. The longitudinal musculature is especially well developed near the outer surface of the middle lobe, near the base (Figs. 49, 50, 51).

At the base of the groove between the middle and shell or outer lobes there is a recessed region lined by the flattened epithelium of the cells forming the periostracal gland (Fig. 50). There is a transitional region between the ciliated epithelial cells of the outer surface of the middle lobe and these cells; so that cells with long cell extensions surrounded by secreted periostracum, as well as cilia, are seen on the external surface of the middle lobe near the gland (Fig. 51). The cytoplasm of cells forming the gland is packed with glycogen, there is a Golgi apparatus near the nucleus, and



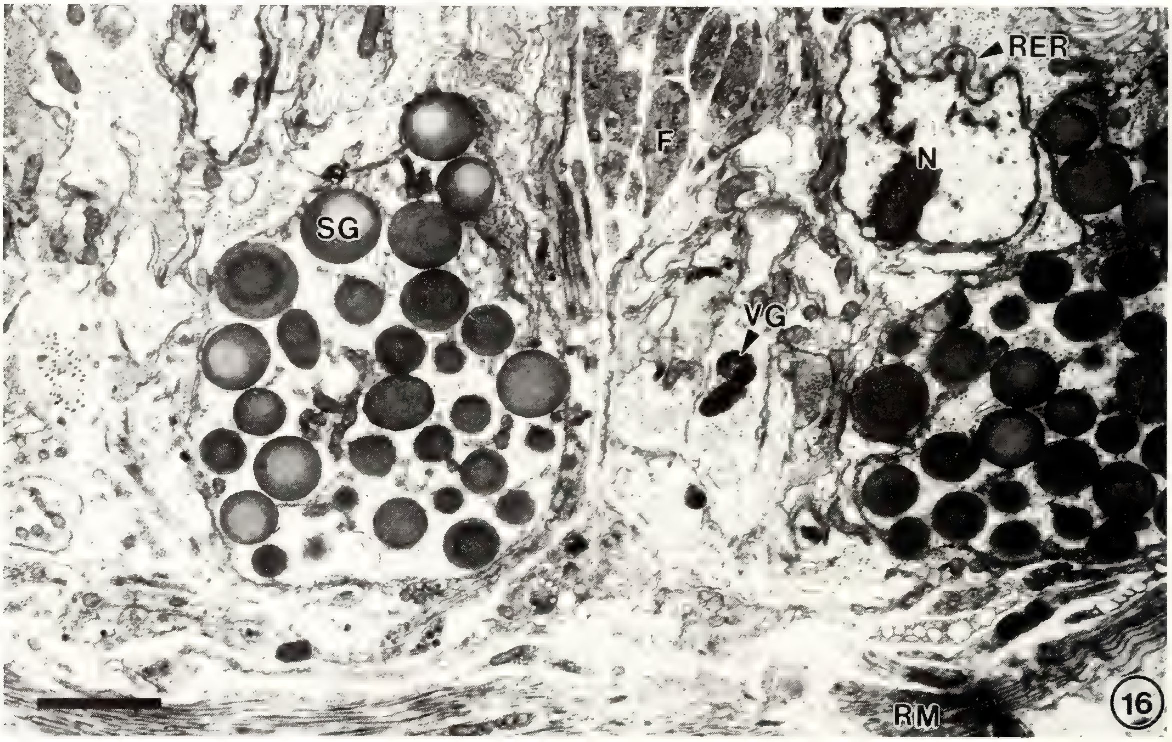
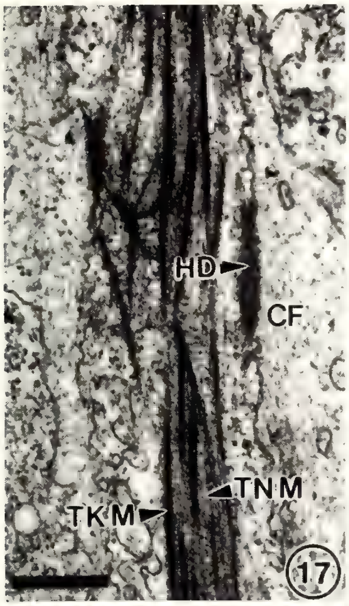
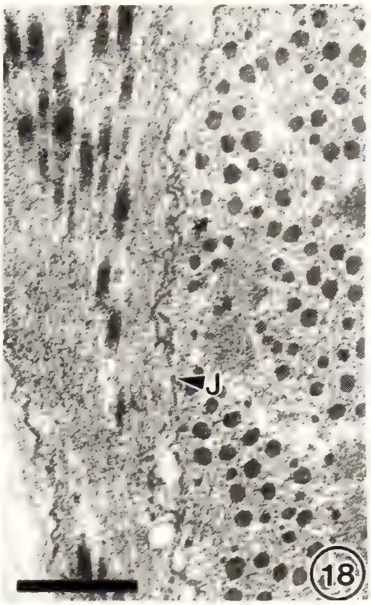
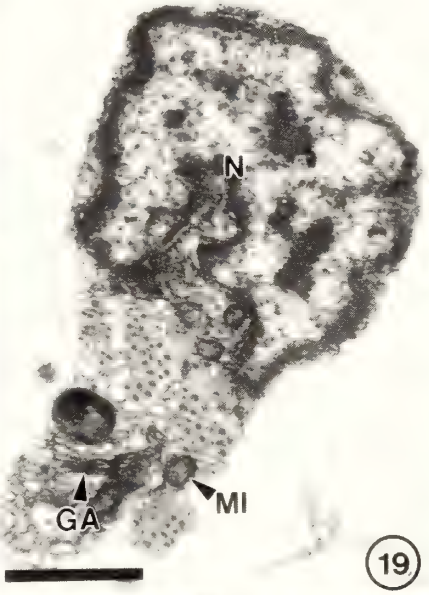


Fig. 15. SS of mantle. L.S. The epithelial cells have microvilli at the apex. They usually contain membrane bound vesicles with darkly staining inclusions of varying shape and size, and sometimes lipid droplets. There is abundant glycogen in the cytoplasm, which is more densely packed in some cells than others. There are mucous cells between the epithelial cells, and beneath the epithelium subepithelial muscle fibres and an amoebocyte are present (K, MS, TEM, scale bar = 2 μm). **Fig. 15: insert.** This shows part of the same specimen at a higher magnification. Infoldings of the basement membrane form cisternae of smooth endoplasmic reticulum, some of which are filled with dark material and extend towards the apex of the cell. These infoldings alternate with cisternae of rough endoplasmic reticulum (scale bar = 1 μm). **Fig. 16.** L.S. of SS of mantle, near lobes. This portion of the mantle has contracted, in spite of treatment with magnesium sulphate. There are small subepithelial muscle fibres seen in T.S. in folds of the epithelium, as well as secretory cells containing distinct granules. Below the epithelium large radial muscle fibres are visible (K, MS, TEM, scale bar = 2 μm).







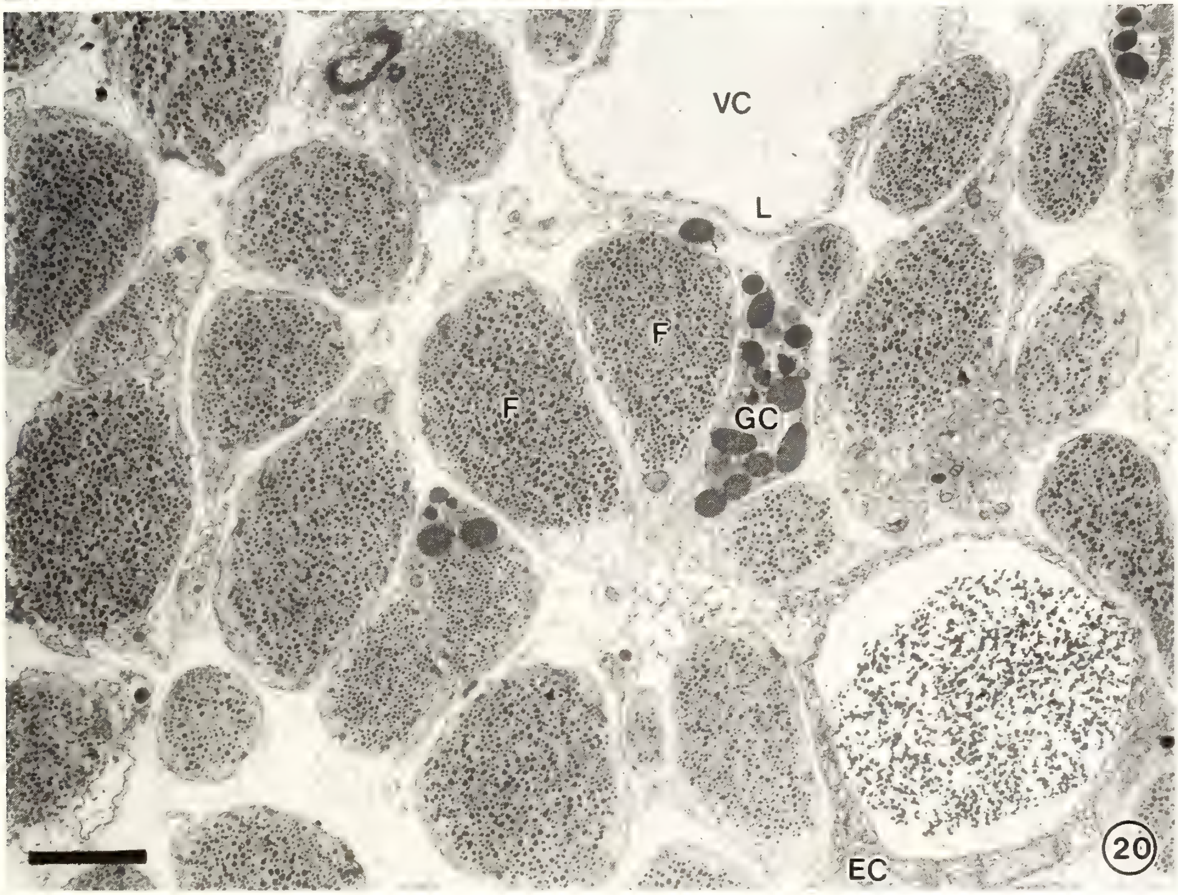
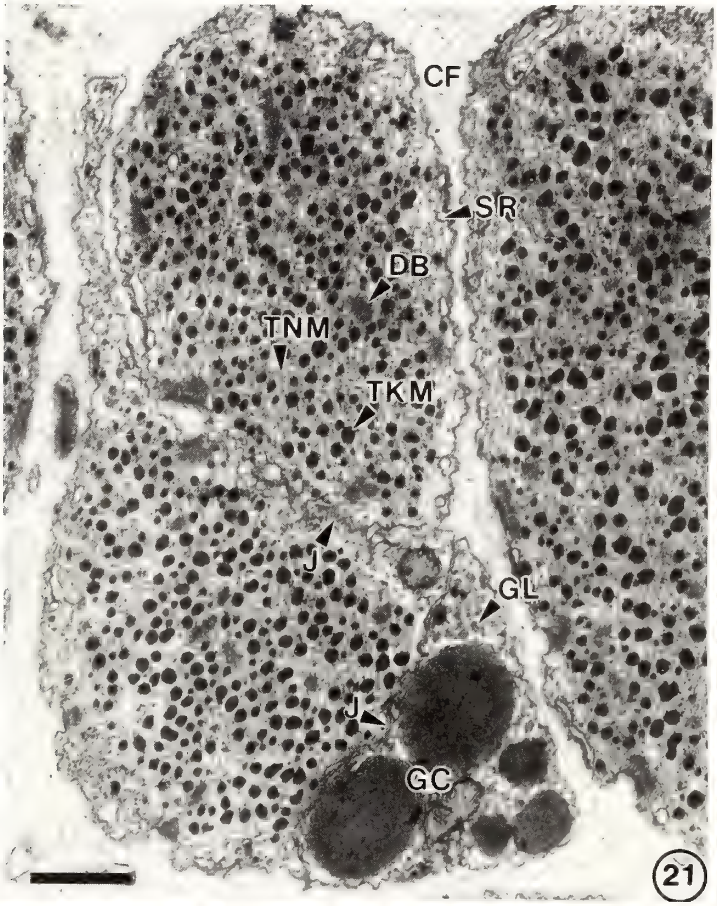
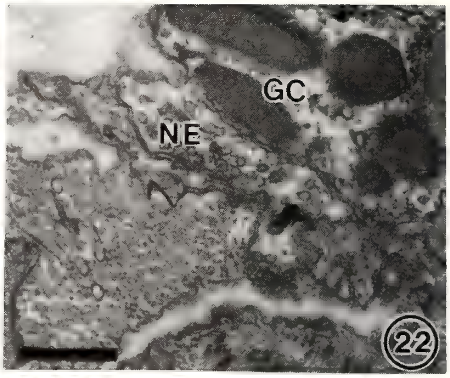
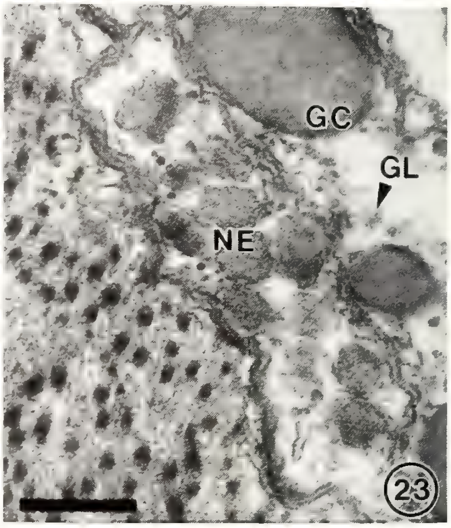
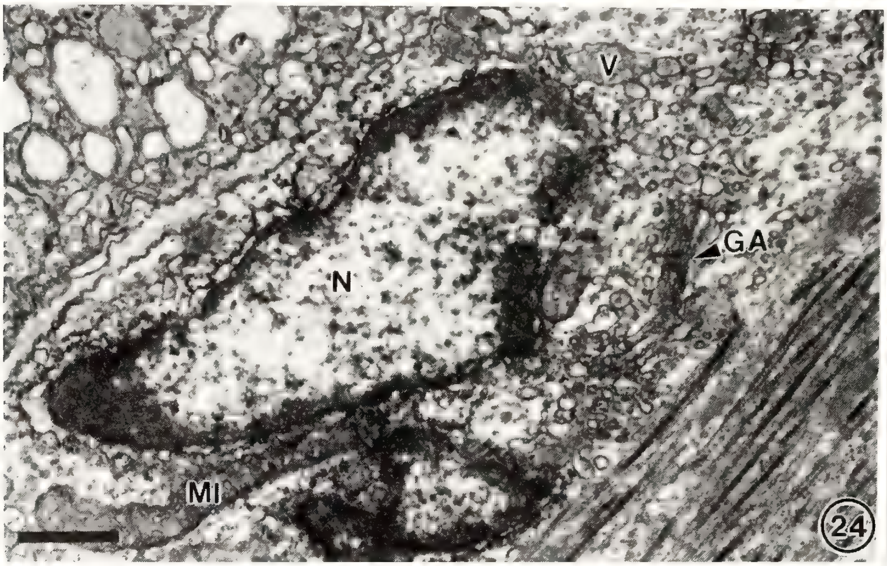


Fig. 17. L.S. of subepithelial muscle fibre near PS of mantle. Thick and thin myofilaments are visible. Collagen fibres are attached to the sarcolemma where there is a hemidesmosome (K, MS, TEM, scale bar = 500 nm). **Fig. 18.** SS of mantle. Sarcolemmas of two subepithelial muscle cells are closely apposed, forming a junction (K, MS, TEM, scale bar = 300 nm). **Fig. 19.** PS of mantle. A subepithelial muscle cell is shown in cross section. The nucleus is situated to one side of the cell, and cross sectioned myofilaments, a Golgi apparatus and mitochondria are present in the cytoplasm (K, MS, TEM, scale bar = 1 μm). **Fig. 20.** T.S. of radial muscle near SS of mantle. The fibres are larger than those of the subepithelial muscle fibres, and glial cells are often closely associated with them. Endothelial cells surround a capillary, and a lipid-containing vesicular cell is present (K, MS, TEM, scale bar = 2 μm).









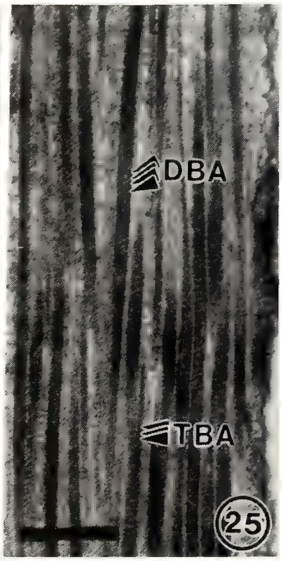


Fig. 21. T.S. of radial muscle. Thick and thin myofilaments as well as dense bodies can be seen in the muscle fibre. There are small vesicles of sarcoplasmic reticulum beneath the sarcolemma. There is a junction between two muscle cells, and between one of these cells and a glial cell containing glycogen. Collagen fibres are present between the muscle fibres (K, MS, TEM, scale bar = 500 nm). **Fig. 22.** Radial muscle. There is a nerve ending containing clear vesicles, accompanied by a glial cell, next to the sarcolemmas of two muscle fibres (K, MS, TEM, scale bar = 500 nm). **Fig. 23.** This nerve ending contains large, dense vesicles. The accompanying glial cell contains glycogen rosettes (K, MS, TEM, scale bar = 300 nm). **Fig. 24.** A nucleus is present in the cytoplasm to one side of the myofilaments of a radial muscle cell. There is also a Golgi apparatus, mitochondria and vesicles (K, MS, TEM, scale bar = 500 nm). **Fig. 25.** L.S. radial muscle. The thick myofilaments show transverse and diagonal banding (K, MS, TEM, scale bar = 500 nm).

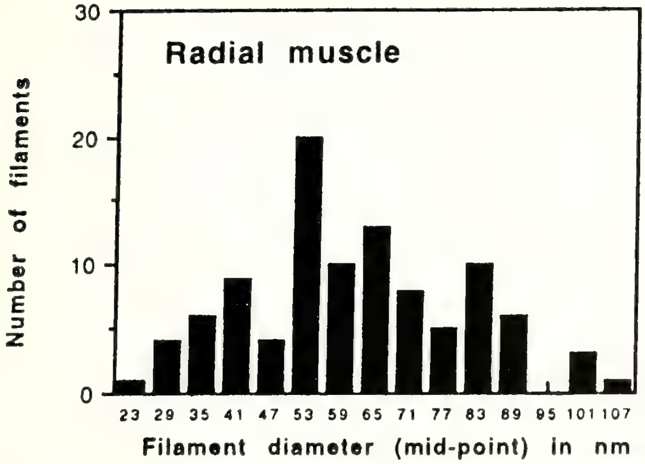


Fig. 26. Graph showing the diameters of the thick myofilaments in the radial muscle of the mantle. The diameters are plotted in categories of 6 nm. The mode is in the category of 50-56 nm, with a mid-point of 53 nm.

there are membrane-bound granules with light and dark inclusions as well as mitochondria (Fig. 52). The apical cytoplasm contains many vacuoles and has many long cytoplasmic processes, each surrounded by a layer of periostracum so that a multilayered, but very thin periostracum is secreted (Figs. 51, 52, 53, 54). This extends over the inner surface of the outer lobe, which consists mainly of epithelial cells with microvilli, although a few cilia are present (Figs. 55, 56).

Thick and thin myofilaments and dense bodies can be distinguished in the muscle fibres proximal to the gland (Fig. 57). The thick myofilaments are cross-striated, with some indications of diagonal banding, and the dense bodies situated at the sarcolemma form hemidesmosomes (Fig. 58).

The epithelial cells of the inner surface form crypts with secretory globules at the surface (Figs. 55, 56, 59). These crypts are lined by cuboidal cells with many vesicles in the apical cytoplasm (Fig. 60). Many goblet shaped secretory cells are present, most of which are of the type containing discrete, dark granules; but others are more like typical mucous cells. The bodies of at least some of these cells extend below the epithelium, and are sometimes closely associated with each other (Fig. 61). The lower surface of the outer or shell lobe has cells with many apical vesicles, and vesicles with electron-dense contents (Fig. 62), but few goblet cells.

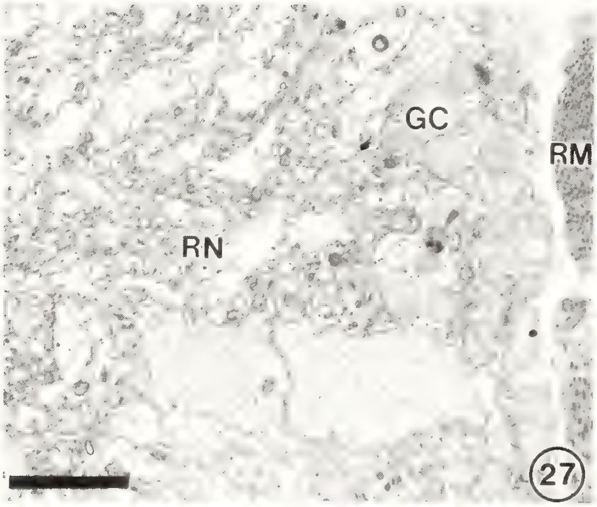
The base of the outer lobe was contracted in this specimen and, as in the shell surface of the contracted mantle, muscle fibres are seen in cross section between the bases of the epithelial cells of the inner and outer surfaces (Figs. 59, 62), as well as in all directions within the lobe. They are accompanied by glial cells, nerve axons and neuromuscular endings. The sarcolemmas of adjoining muscle fibres are often parallel and close together, and form junctions (Fig. 63). Sometimes there is an orderly arrangement of one row of thin myofilaments around each thick myofilament (Fig. 64). From 81 measurements of the thick myofilaments, the widest myofilament was 80 nm in diameter, and the thick myofilaments had a mean width of 42 and a median width of 41 nm. The mode was 36-37 nm.

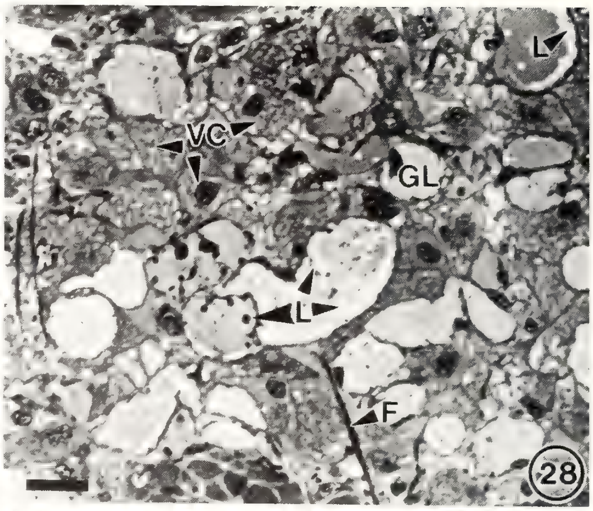
DISCUSSION

As mentioned above, this study is an overview of the structure of the mantle and its lobes, and many areas need more detailed study. Vesicular cells containing lipid and glycogen are found in the connective tissue of the mantle and its lobes, as described by Galtsoff (1964). According to Galtsoff (1964) and other workers (Bargeton, 1942; Gabbott, 1975), the amount of glycogen is variable, decreasing as the gonads develop, so the cells filled with small vesicles and those filled with glycogen could be different forms of each other, the prevalence of each type depending on the amount of glycogen stored in the mantle. Two types of storage cells have been described in the mantle of *Mytilus edulis* L. The ''glycogen cell (=vesicular connective-tissue cell)'' is similar to the cells described above, whereas the cells containing lipid droplets in the oyster could correspond to adipogranular cells (Lenoir *et al.*, 1989). According to Gabbott (1975), the main energy reserve in the bivalve egg and larva is lipid, which decreases during metamorphosis and early spat growth, whereas the level of glycogen increases as the spat develops. The main energy reserve in the adult is glycogen. Further study of the relationships between the different types of storage cells in the oyster, and their variations at different times of year, is needed.

Galtsoff (1964) describes fusiform cells, which appear to be equivalent to the small muscle fibres found crossing the mantle in our study, since they would be difficult to identify as muscle cells without electron microscopy. He also describes longitudinal muscle fibres and elastic fibrils, the latter being more abundant at the free edge and beneath the surface epithelium; these could both be the subepithelial muscle fibres described in this account. This arrangement of small muscle cells is similar to that described in *Mercenaria mercenaria* (Linnaeus, 1758) by Neff (1972b). Small arteries lined by an endothelium and elastic tissue; veins lacking the endothelium, with little elastic tissue, and freely wandering blood cells or ameobocytes were also found in the connective tissue, as described by Galtsoff (1964).

Two types of goblet shaped secretory cells were found in the epithelium of the mantle and mantle lobes of *Crassostrea virginica*, as described by Galtsoff (1964). One, described by Galtsoff as containing eosinophilic granules, has distinct dark granules; the other, described by Galtsoff as a mucous cell, has more closely packed granules that tend to coalesce. Mucins are vitally important for a variety of func-





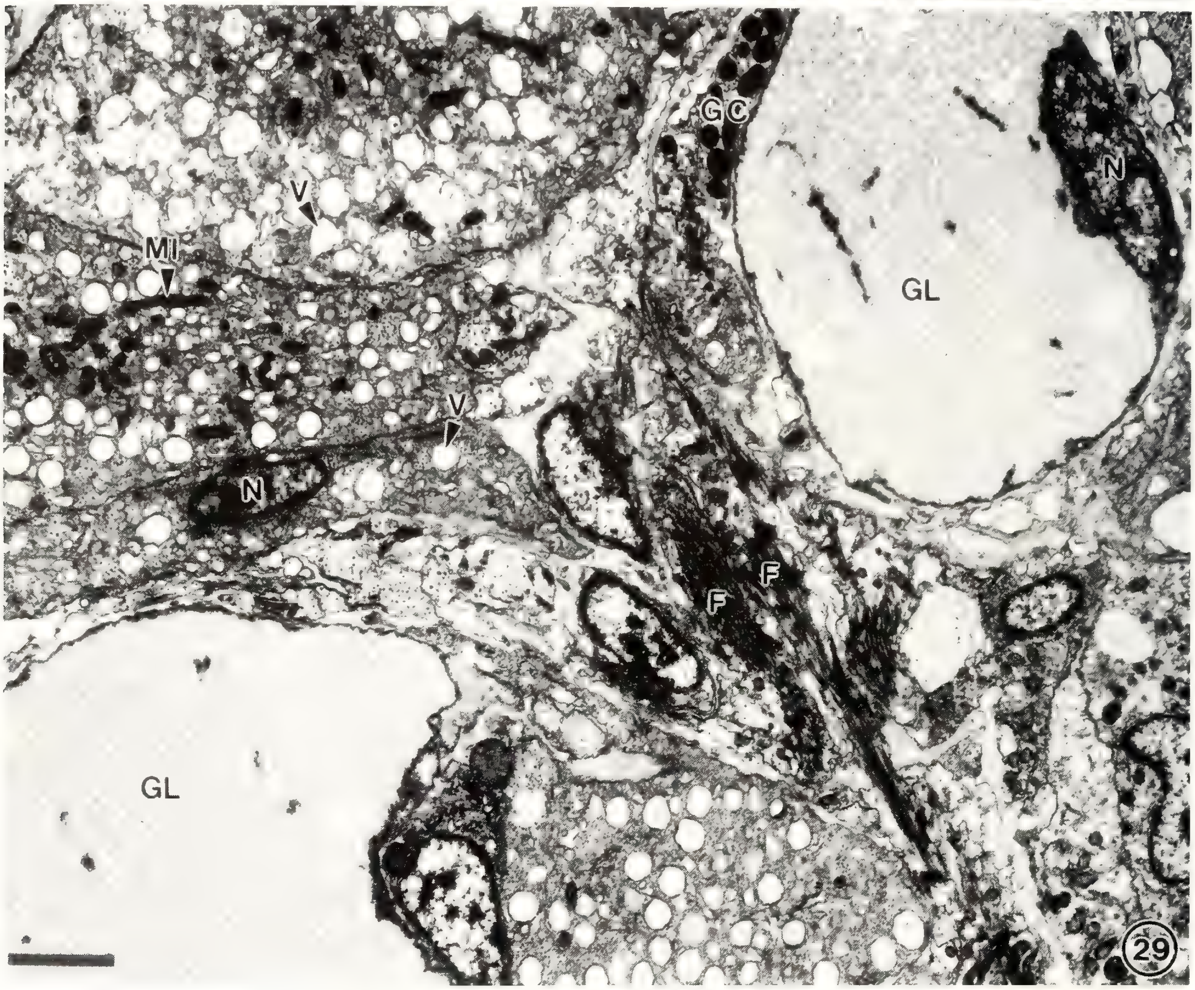
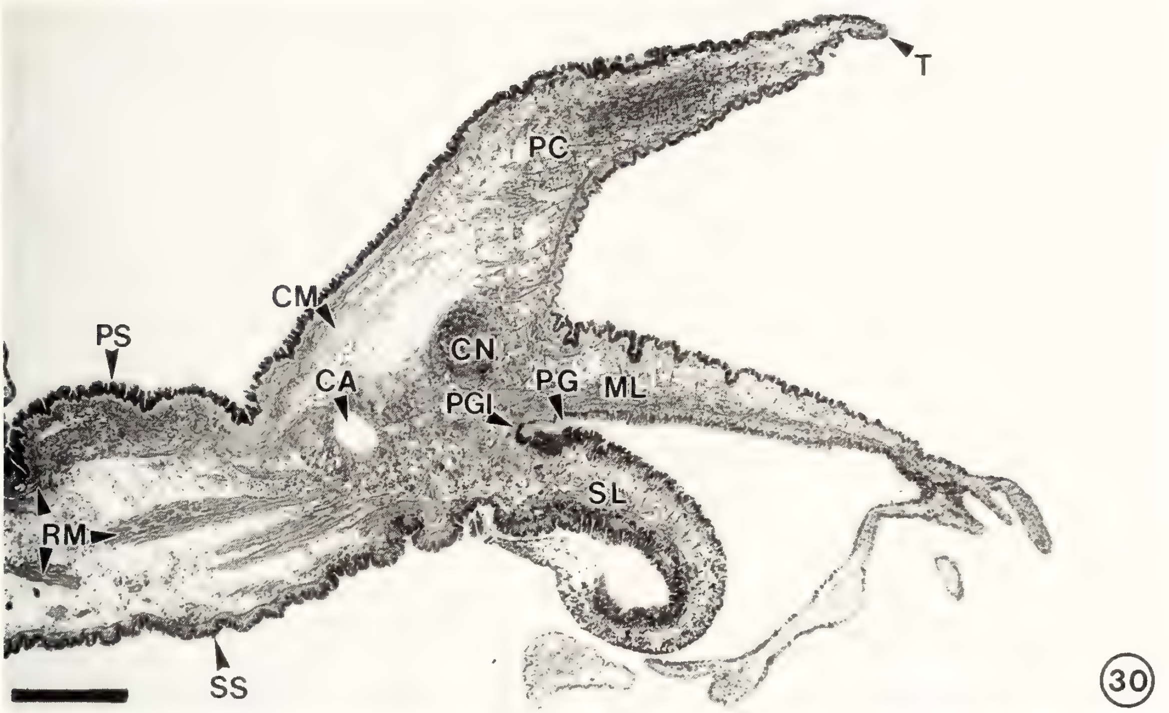


Fig. 27. L.S. radial nerve. There is a layer of glial cells at the surface of the nerve, which consists of unmyelinated axons and nerve-endings containing neurofilaments and a variety of vesicles (K, MS, TEM, scale bar = 2 μm). **Fig. 28.** Mantle. Cells with a vesicular cytoplasm, and cells with large areas of homogenous cytoplasm are present. Dark and light lipid droplets can be seen in some of these. 0.5 μm (K, MS, scale bar = 10 μm). **Fig. 29.** Centre of mantle. The vesicular cells contain many vesicles and mitochondria, with glycogen in the cytoplasm between. Other cells are filled with a large mass of glycogen, and most of the cell organelles are pushed to the periphery. Small muscle fibres contain a central core of myofilaments, and are oriented in various directions. Glial cells are also present (K, MS, TEM, scale bar = 2 μm).



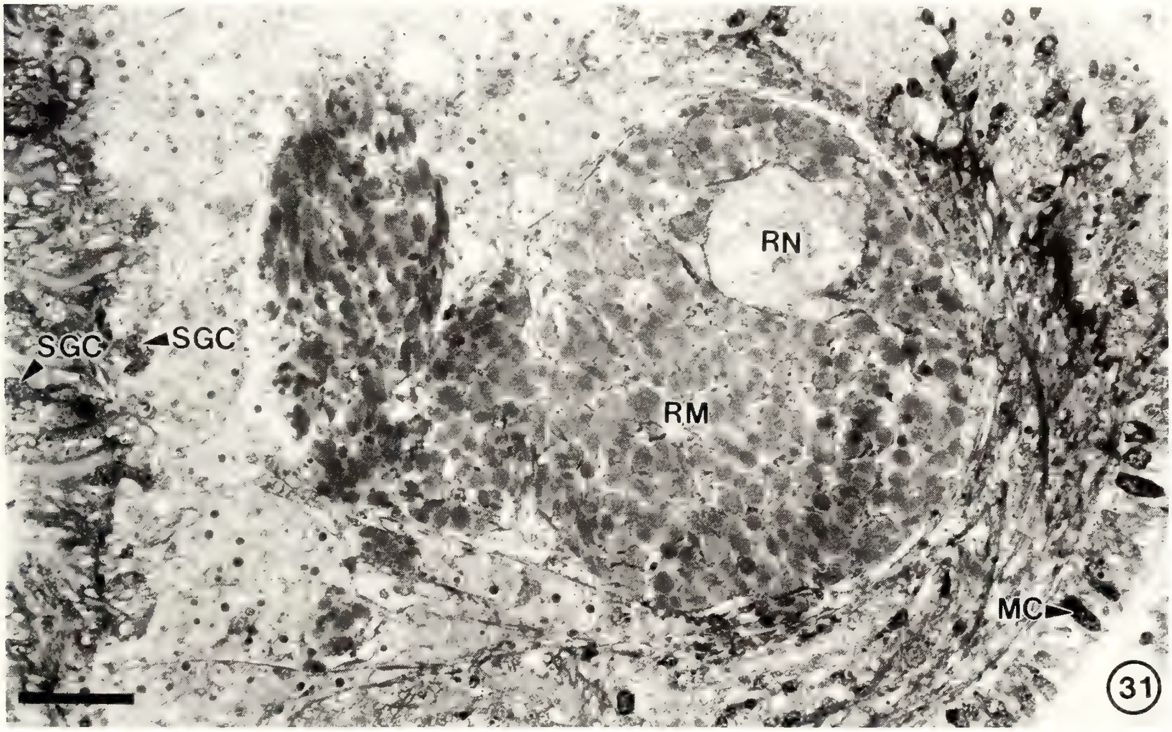
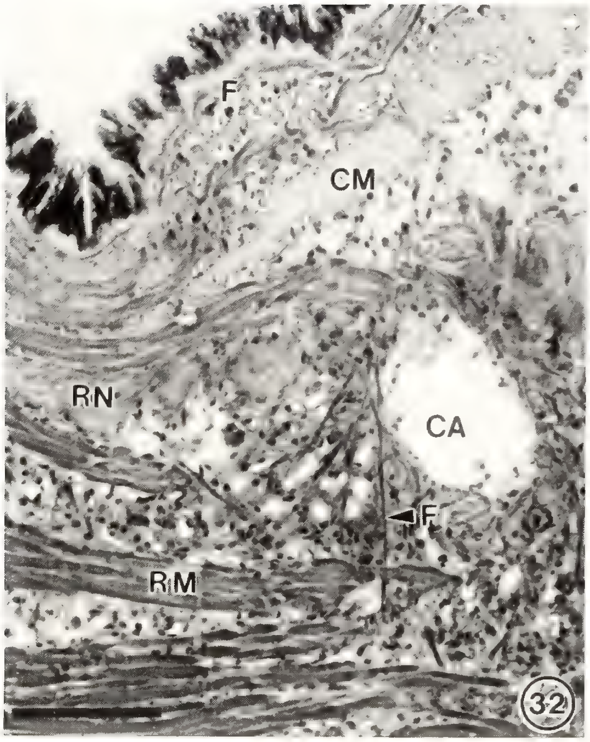
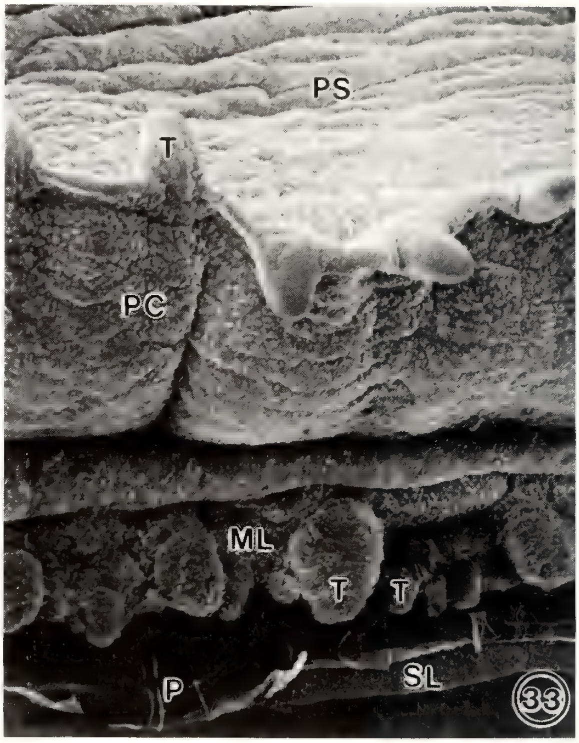


Fig. 30. L.S. outer edge of mantle and lobes, pallial surface dorsal. The mantle is divided into the inner lobe or pallial curtain, middle or sensory lobe and outer or shell lobe. The circumpallial nerve and artery are at the base of the lobes, and there is a circular muscle above these. The periostracal gland is at the base of the periostracal groove between the middle and shell lobes. Radial muscle fibres extend through the mantle, and some fibres continue into the lobes. Tentacles extend from the middle and inner lobes (IG4F, MS, JB4, CMB, scale bar = 0.3 mm. **Fig. 31.** T.S. base of lobes. Pallial surface at right, shell surface at left. Secretory cells containing distinct granules and mucous cells can be seen at both surfaces of the mantle. The secretory cells on the shell surface often extend below the epithelium. The radial nerve is surrounded by the radial muscle, which is large and extends across most of the mantle (IG4F, 0.5 μm, scale bar = 50 μm).





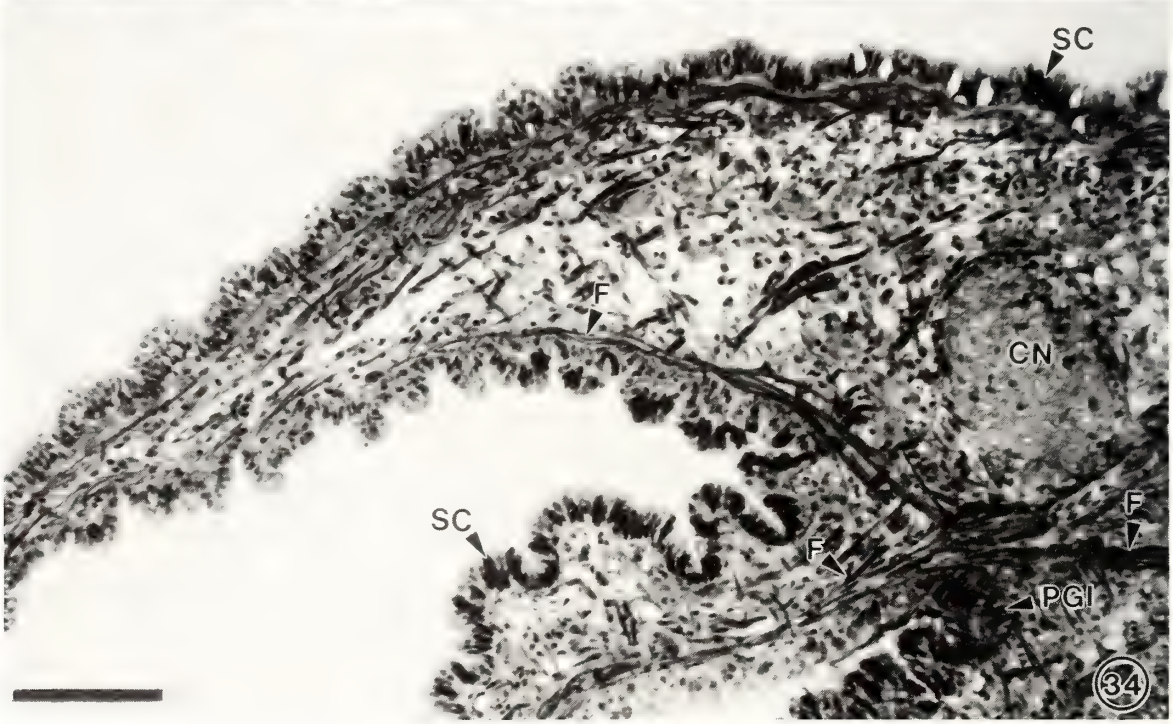


Fig. 32. L.S. base of lobes. Radial muscle fibres extend across most of the mantle, and a circular muscle is present near the pallial surface. The radial nerve, circumpallial artery, small subepithelial muscle fibres and muscle fibres passing across the mantle are also visible (1G4F, MS, JB4, CMB, scale bar = 0.1 mm). **Fig. 33.** Lobes at edge of mantle. The lobes and tentacles are contracted in this specimen. The inner lobe with its tentacles extends up into the mantle cavity. The middle lobe has large tentacles with small, slender tentacles between. The periostracum extends from the periostracal groove over the inner surface of the outer or shell lobe (1G4F, SEM, scale bar = 0.3 mm). **Fig. 34.** L.S. inner lobe and bases of middle and outer lobes. Muscle fibres extend from the radial muscle into the lobes, and also run obliquely and transversely in the lobes. Goblet shaped secretory cells are concentrated near the base of the inner lobe, and the inner surface of the middle and outer lobes (K, MS, JB4, VG, scale bar = 0.1 mm).

tions in bivalves, including feeding, cleansing, protection, shell formation, and dispersal (Prezant, 1985 and 1990). Simple ''goblet'' cells, the same height as the surrounding epithelium, are common in the epidermis of molluscs. They show great variability in the chemistry of their secretions, but most are mucus-secreting cells (Franc, 1960; Storch and Welsch, 1972; Machin, 1977). Mucus is primarily water, and consists of mucopolysaccharides or glycoproteins with protein and carbohydrate portions (Prezant, 1985). Some goblet cells contain a structureless mass, but some, like those described here, contain dark, membrane-bound granules, which have a denser core in some cells. The granules usually arise in the Golgi area, but can originate from the rough endoplasmic reticulum. The membrane can remain intact until the granule is discharged, or the granules can coalesce before they are discharged (Storch and Welsch, 1972; Machin, 1977). The cells with distinct, dark granules found in *C. virginica* seem to be of the first type, whereas the cells with lighter granules are of the latter type. Histochemical tests are needed to determine the nature of the goblet shaped secretory cells of *C. virginica*, and would probably reveal more than the two types recognised morphologically.

The distribution of the ciliated epithelial cells on the pallial surface is similar to that reported in the fresh-water mussel, *Amblema plicata* Conrad (Petit *et al.*, 1978) and the tellin, *Fabulina nitidula* (Dunker) (Kawaguti and Ikemoto, 1962). Beneath the epithelium is an ''elastic basal membrane'' according to Galtsoff (1964), which is the thick basement membrane shown in this study. In specimens with the radial muscle contracted, this membrane appears to prevent the bases of the epithelial cells of the pallial surface lifting into the folds; whereas the bases of the epithelial cells of the shell surface and of the mantle lobes are drawn up into the folds, which then surround groups of subepithelial muscle fibres.

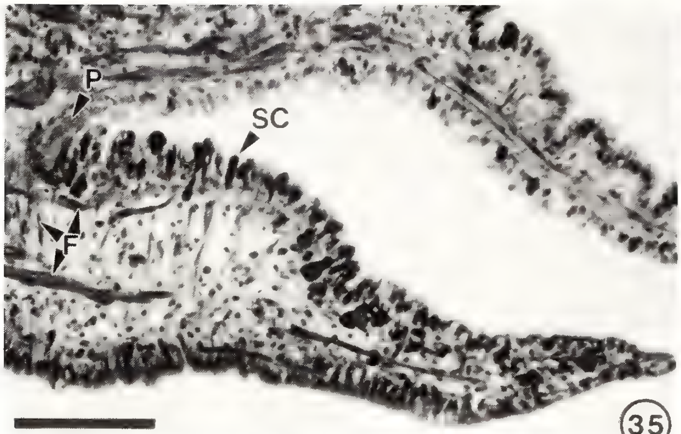
The radiating form of the radial muscle has been shown in drawings by Galtsoff (1964). According to Galtsoff, the high contractile ability of the mantle is related to the presence of the conspicuous radial and concentric musculature, as well as smaller longitudinal and transverse muscles. There appear to be junctions between these muscle fibres, as well as regions where the sarcolemmas are closely apposed. Junctions were not found in the adductor muscle of *Crassostrea virginica* (Morrison, 1992), but have been described in other molluscan muscles (Twarog *et al.*, 1973; Nicaise and Amsellem, 1983).

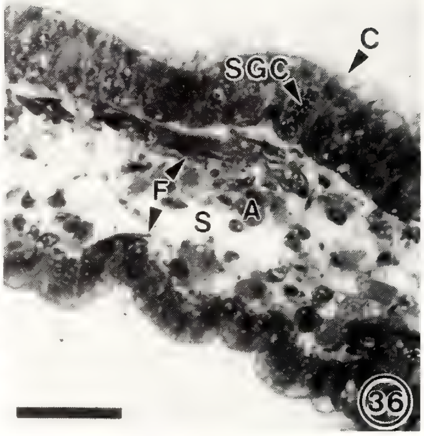
The muscles of the mantle and its lobes are described as smooth, non-striated by Galtsoff. The thick myofilaments of the radial muscle are similar in width to those of the opaque part of the adductor of *Crassostrea virginica*, and have similar, though not as clear, cross and diagonal striations, which are typical of paramyosin (Morrison and Odense, 1974; Morrison,1992). The radial muscle fibres are similar in diameter to the smaller axis of the flattened fibres of the translucent adductor muscle, but are much smaller than those of the opaque adductor muscle. It would be interesting to know what the differences are between the radial and adductor muscles, since the structure and arrangement of the myofilaments are similar, but the adductor can exhibit ''catch''. The thick myofilaments of the subepithelial muscles and the muscles in the mantle lobes, although not as wide as those of the radial muscle, are wider than those of the translucent, obliquely striated muscle of the adductor, which have a mean width of 32 nm (Morrison, 1992). The dense bodies of these muscles sometimes show oblique orientation, although the myofibrils are so small that this can only be followed for a short distance. The thin myofilaments of molluscan muscle appear to be similar to the actin filaments in other groups of animals (Heyer *et al.*, 1973).

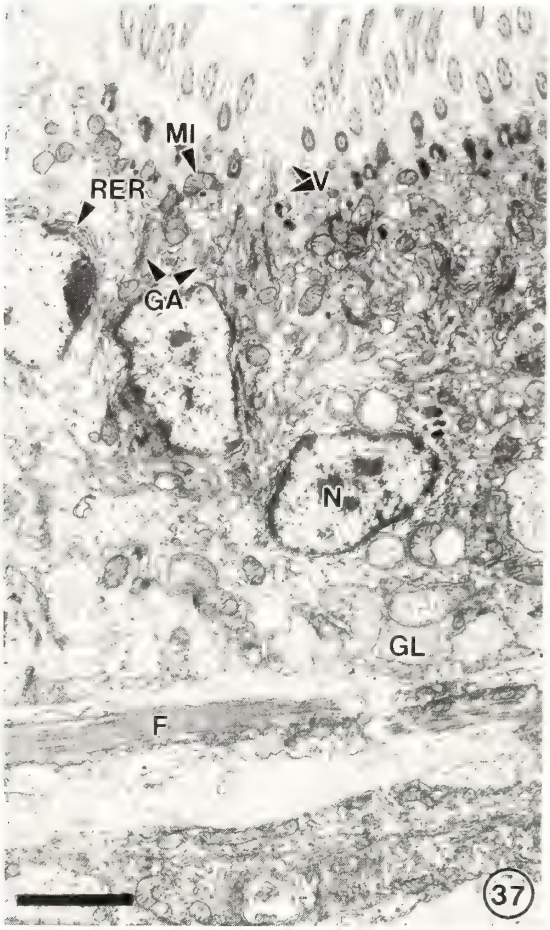
In this study two types of vesicles, about 70 and 160 nm in diameter, were found in neuromuscular junctions of the radial muscle. Possibly this is morphological evidence for the dual innervation indicated by physiological studies on the mantle of the bivalve *Spisula solidissima* (Dillwyn) (Wilson, 1969); although in the latter study only nerve endings containing numerous agranular vesicles were described. A variety of clear and dense vesicles, that could be associated with the presence of different neuromuscular transmitters, have been described in mollusc muscle (Heyer *et al.*, 1973; Nicaise and Amsellem, 1983). A similar distribution of vesicles to that found in this study has been reported in *Mytilus* anterior byssus retractor muscle (McKenna and Rosenbluth, 1973). The nerves and nerve-endings are accompanied by cells of the glio-interstitial network, which have been described in the muscles of various molluscs, and are generally more conspicuous in marine species (Nicaise and Amsellem, 1983). They have been described in the adductor muscle of *Crassostrea virginica* (Morrison, 1992).

The isolated mantle of the *Crassostrea virginica* is capable of laying down both the inorganic (mainly calcium carbonate) and organic (conchiolin) components of the shell, and the movement of calcium and bicarbonate ions across it has been studied (Jodrey and Wilbur, 1955; Wilbur, 1972, 1985; Machin, 1977; Crenshaw, 1980; Simkiss and Wilbur, 1989). The shell surface of the mantle is highly permeable to these ions, which are transported through the epithelium of the shell surface into the extrapallial space for shell formation. The ion exchange probably takes place in both directions, depending on whether shell is being laid down or whether it is being dissolved. The latter occurs in anaerobic conditions, when acids form as a result of metabolism and dissolve intracellular deposits of calcium carbonate and the inside of the shell. The spicules found on the shell surface of the mantle (using SEM) could result from precipitation of ions from the extrapallial space during specimen preparation.

Galtsoff (1964) demonstrated alkaline phosphatase in the epithelium, and stated that both conchiolin-secreting and







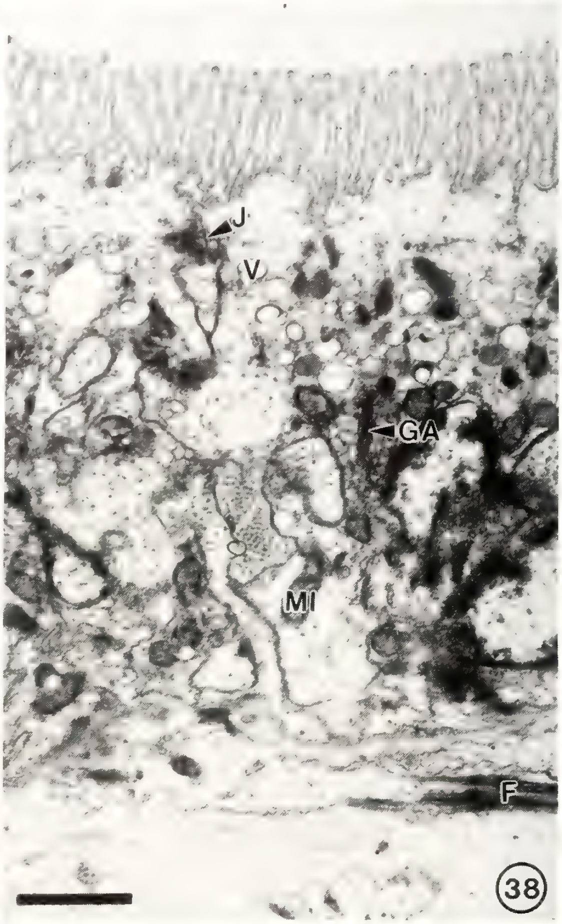
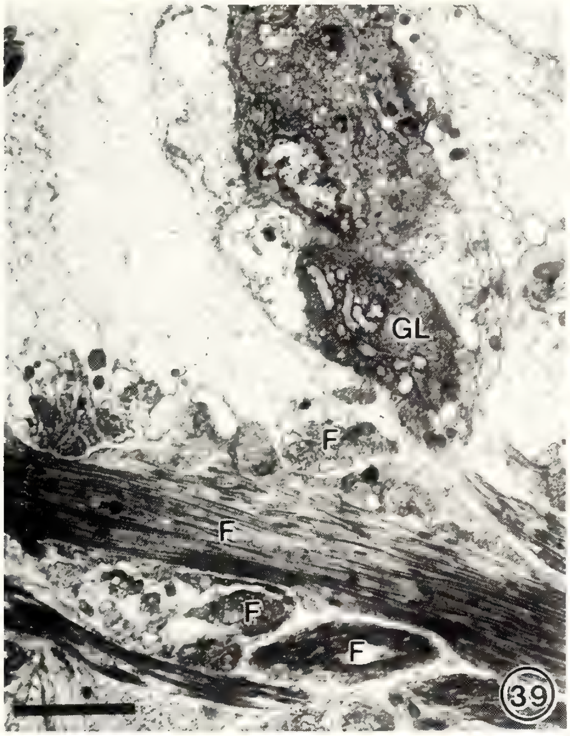
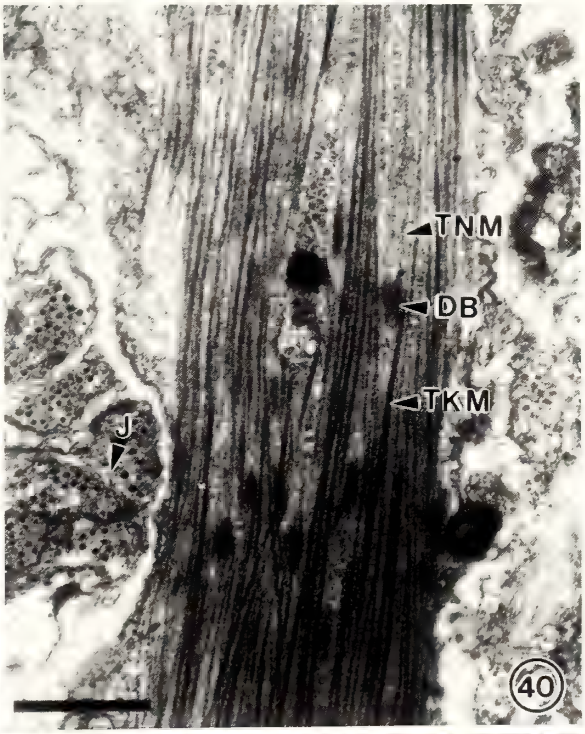
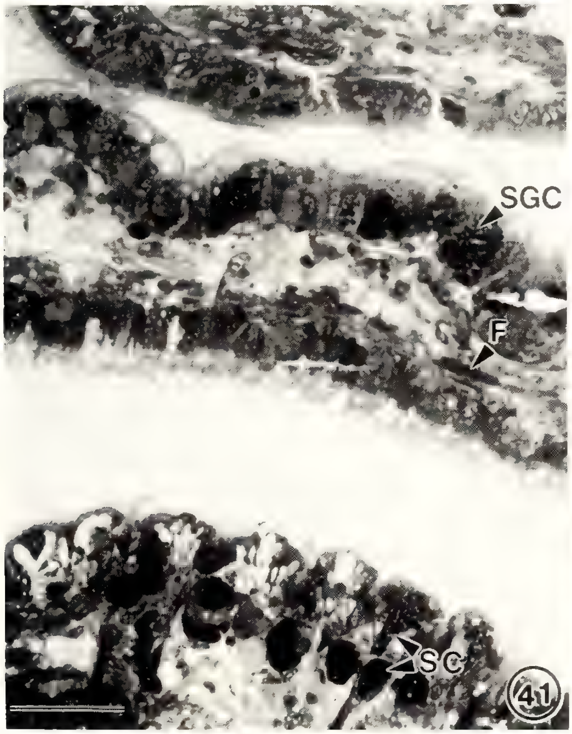


Fig. 35. L.S. middle and outer lobes. The periostracum is forming at the base of the periostracal groove. Many muscle fibres are present near the base of the gland as well as in the lobes. Goblet shaped secretory cells are concentrated on the inner surfaces of the lobes, and some extend below the epithelial surface of the outer lobe (K, MS, JB4, CMB, scale bar = 0.1 mm). **Fig. 36.** L.S. inner lobe. There are small subepithelial muscle fibres next to the pallial or inner surface, which is heavily ciliated, and the outer surface, which has fewer cilia. There is a secretory cell with distinct granules (K, MS, 0.5 μm, scale bar = 30 μm). **Fig. 37.** Inner surface of inner lobe. The epithelial cells possess cilia and microvilli. Mitochondria, several elements of Golgi apparatus, rough endoplasmic reticulum and vesicles are present in the apical cytoplasm of each cell. Glycogen is more abundant in some cells than others. A layer of subepithelial muscle fibres is present (K, MS, TEM, scale bar = 2 μm). **Fig. 38.** Outer surface of inner lobe. Few cilia are present on the epithelial cells, and none are seen in this micrograph. Large clear vesicles and vesicles with dark contents are present in the apical cytoplasm, and there is a Golgi apparatus and several mitochondria near the nucleus. There is a prominent desmosome in the apical junction, and the adjacent plasmalemmas are convoluted. Subepithelial muscle fibres are present (K, MS, TEM, scale bar = 2 μm).







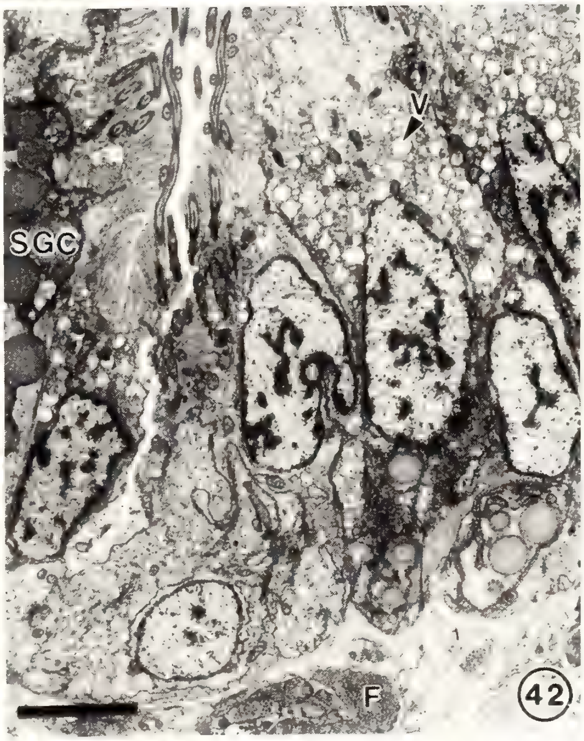
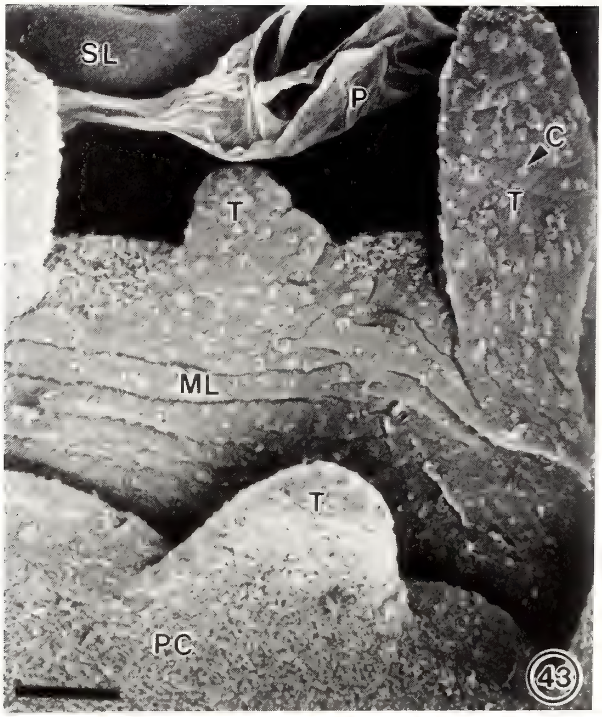
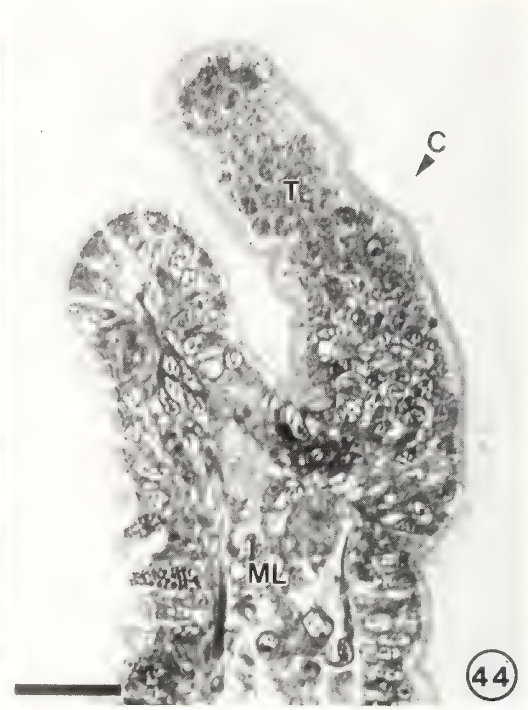
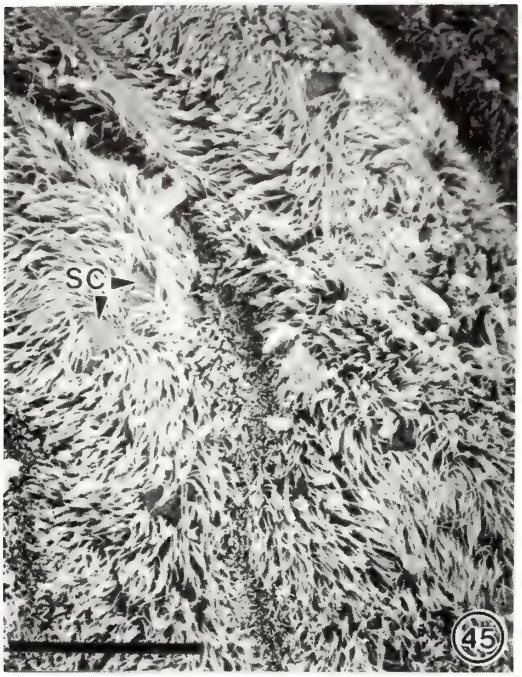
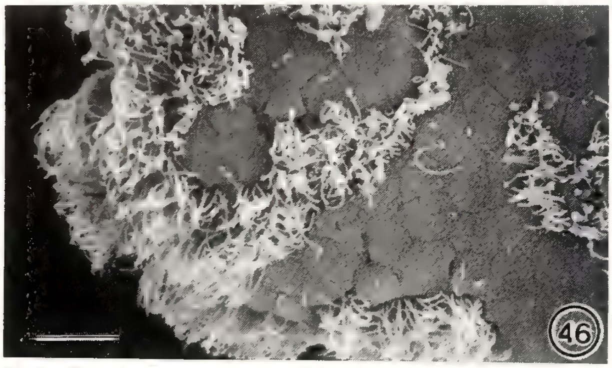


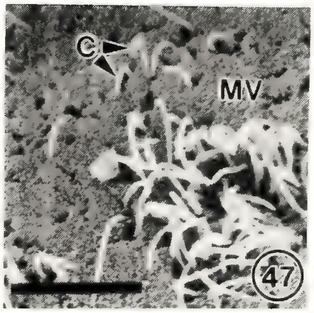
Fig. 39. Centre of inner lobe. Muscle fibres, some being very small, run in all directions. A group of cells containing vesicles, mitochondria and glycogen is present (K, MS, TEM, scale bar = 3 μm). **Fig. 40.** Part of figure 39 at a higher magnification. Thick and thin myofilaments and dense bodies are present in the muscle fibre (K, MS, TEM, scale bar = 1 μm). **Fig. 41.** Middle lobe, outer surface of inner lobe and inner surface of outer lobe. There are many secretory cells on the inner surface of the middle and outer lobes, extending below the epithelium of the outer lobe. Distinct granules can be seen in some of these. The epithelium of the middle lobe is ciliated (0.5 μm, K, MS, scale bar = 30 μm). **Fig. 42.** Middle lobe, inner surface. A secretory cell with distinct granules is present among the epithelial cells, which have cilia as well as microvilli, and many vesicles in the apical cytoplasm. Many of these cells do not reach the basement membrane, giving a partially stratified appearance. Subepithelial muscle fibres are present (K, MS, TEM, scale bar = 3 μm).











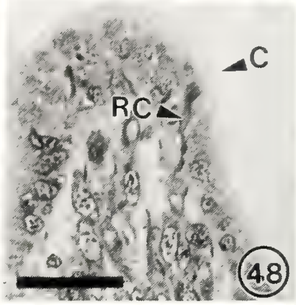
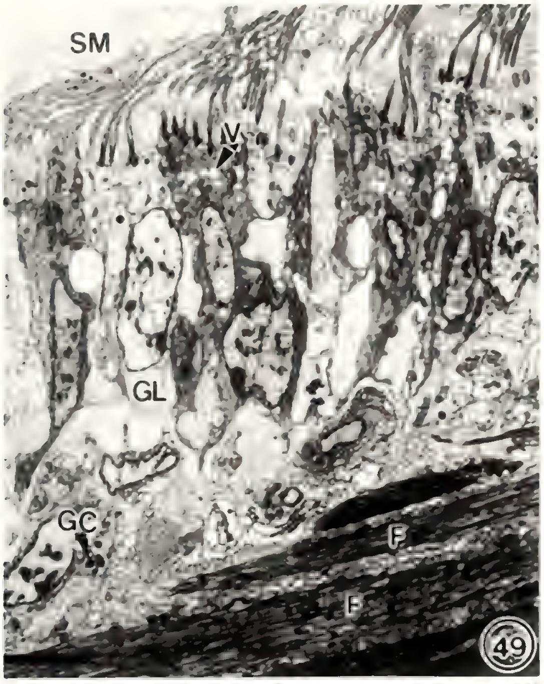
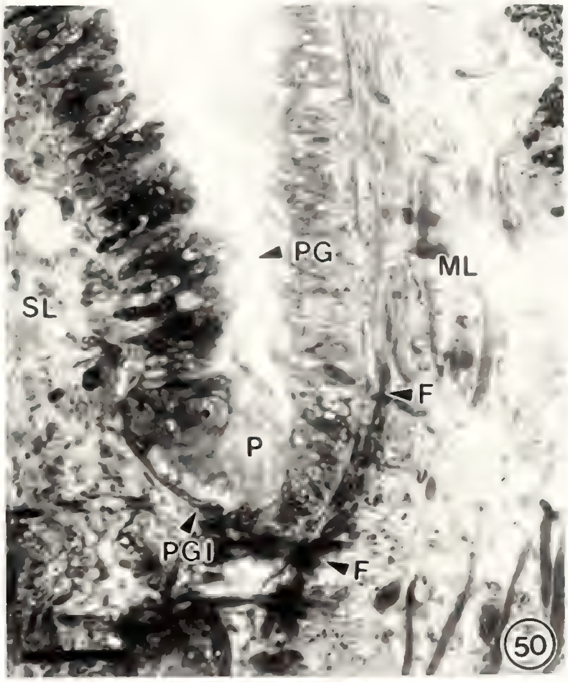
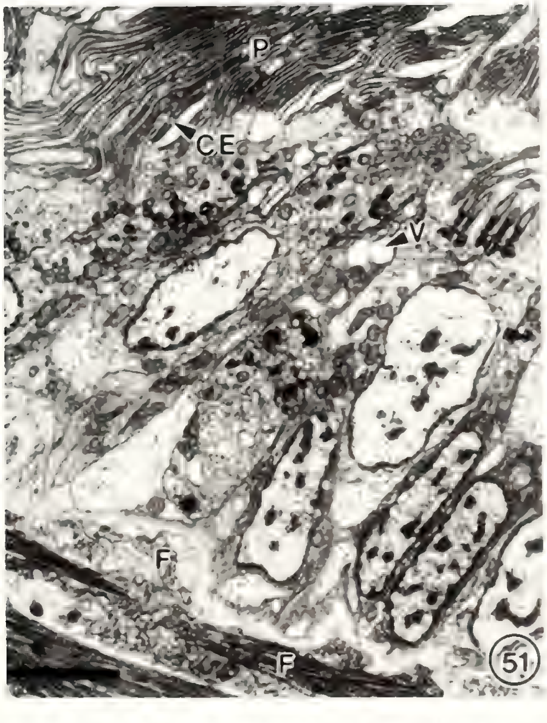


Fig. 43. Lobes at edge of mantle. Tentacles extended. The inner surface of the inner lobe or pallial curtain is heavily ciliated. Groups of cilia can be seen on the surface of the middle lobe and both its large and small tentacles, and the outer edge of this lobe is more heavily ciliated. The outer or shell lobe is unciliated (1G4F, MS, SEM, scale bar = 100 μm). **Fig. 44.** Outer edge of middle lobe, inner surface to the right. The inner surface and the tentacle that extends from it have groups of ciliated cells, whereas the outer edge and outer surface of the middle lobe are well-ciliated. The epithelial cells of the tentacle appear in cross-section, because it is sectioned near its surface (0.5 μm, K, MS, scale bar = 20 μm). **Fig. 45.** Edge of inner lobe. Many cilia are present on the surface. Cells with an unciliated surface, presumably secretory cells, are also present (1G4F, MS, SEM, scale bar = 20 μm). **Fig. 46.** Tip of long tentacle from middle lobe. There are cells with only one or a few cilia, and some, especially at the tip, are heavily ciliated (1G4F, MS, SEM, scale bar = 10 μm). **Fig. 47.** Tip of tentacle from middle lobe. Some cells have only one or two cilia, which face in different directions (1G4F, MS, SEM, scale bar = 5 μm). **Fig. 48.** Tip of tentacle from pallial lobe. A cell with dark cytoplasm and a few cilia, presumably a receptor cell, extends below the epithelial surface (0.5 μm, K, MS, scale bar = 20 μm).







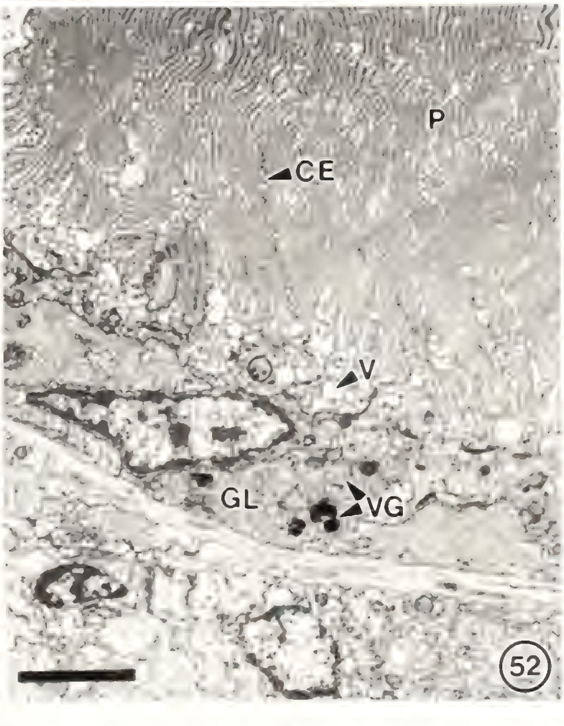


Fig. 49. Middle lobe, outer surface. The epithelial cells have cilia and microvilli, and are covered by a layer of secreted material. These cells contain varying amounts of glycogen, and some have many vesicles in the apical cytoplasm. Blebs from the apical cytoplasm appear to be joining the secretory material. There are many subepithelial muscle fibres (K, MS, TEM, scale bar = 4 μm). **Fig. 50.** Base of periostracal groove, between outer and middle lobes. The periostracal gland consists of flattened epithelial cells at the base of the groove, and periostracum can be seen above it. There is secretory material above the epithelial surface of the middle and outer lobes. Muscle fibres are especially well developed near the outer surface of the middle lobe, and around the periostracal gland (0.5 μm, K, MS, scale bar = 30 μm). **Fig. 51.** Middle lobe, near base. The epithelial cells become more cuboidal towards the periostracal gland, which is to the left of the micrograph, and long cytoplasmic extensions of the apical cytoplasm surrounded by periostracum extend from some of the cells. There are many muscle fibres below the epithelium (K, MS, TEM, scale bar = 3 μm). **Fig. 52.** Periostracal gland. The epithelial cells forming the periostracal gland are small and filled with glycogen, and contain vesicles with darkly staining contents. Long cytoplasmic processes surrounded by periostracum extend from these cells. Numerous clear vesicles are present in the apical cytoplasm (K, MS, TEM, scale bar = 2 μm).

calcium-secreting cells are present, although he found no reliable staining methods for identifying them. Goblet shaped secretory cells are abundant on the shell surface at the periphery of the mantle, at the base of the lobes (Fig. 31), where shell formation is most active (Simkiss and Wilbur, 1989), although few of these cells are found on the shell or outer surface of the outer lobe. Basal invaginations of cells are found where cells are involved in ion transport, as in the chloride cells of fish gills, or the cells lining the urinary tract, so the presence of these in the epithelial cells of the shell surface in *Crassostrea virginica* indicates that these cells could be specialised for the transport of ions. Basal invaginations were also described in the epithelial cells of the shell surface in *Mercenaria mercenaria* (Neff, 1972b). In both *C. virginica* and *M. mercenaria* the thick basement membrane of the pallial surface is lacking, which would facilitate exchange of materials across the epithelium. Most of the calcium in the mantle of bivalves is in a bound form, in spherules or granules, which have been described within intracellular vacuoles and extracellularly (Neff, 1972b; Wilbur, 1972, 1985; Petit *et al.*, 1980), so the dark deposits in the membrane-bound vesicles of the epithelial cells of the shell surface of the oyster mantle and outer lobe could be calcium.

The periostracal groove, as described by Galtsoff (1964), is lined by a single-layered, flattened glandular epithelium. This has been termed the "periostracal gland" (Beedham, 1958), although it does not form a compact body, or have a duct. The cells forming the gland seem to be

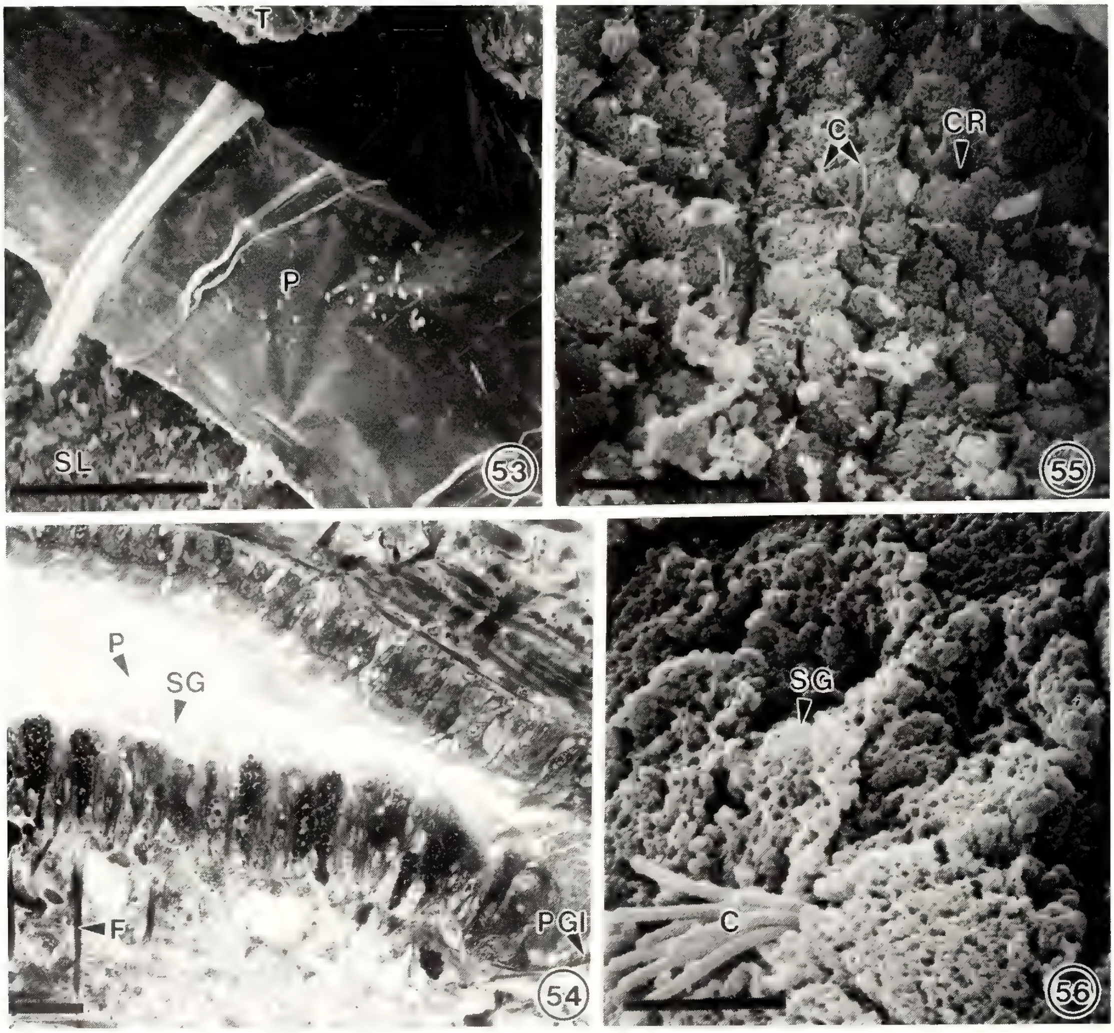
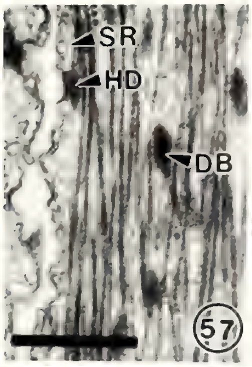
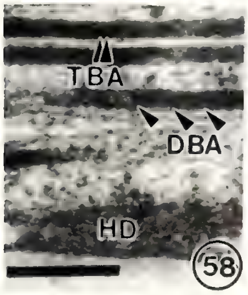
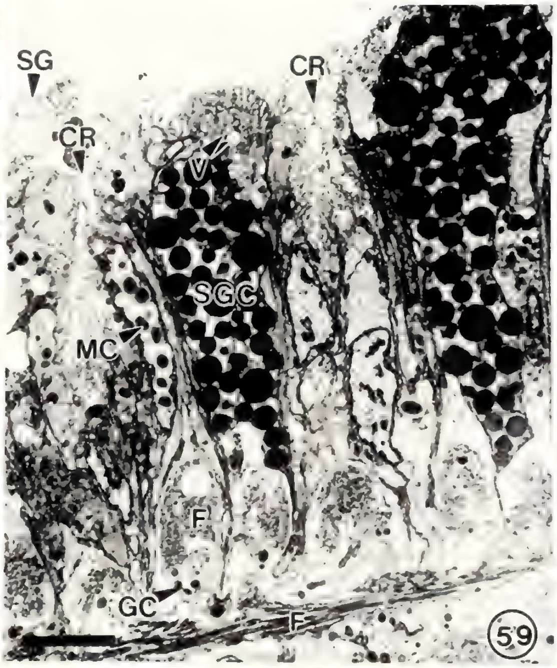
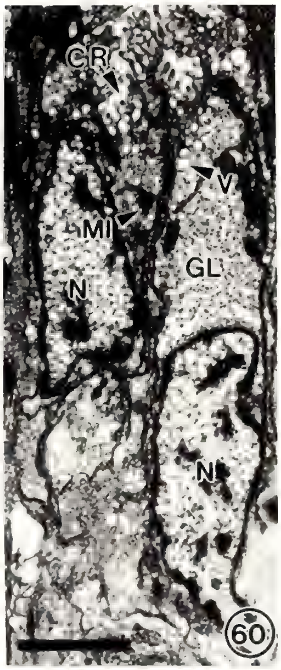


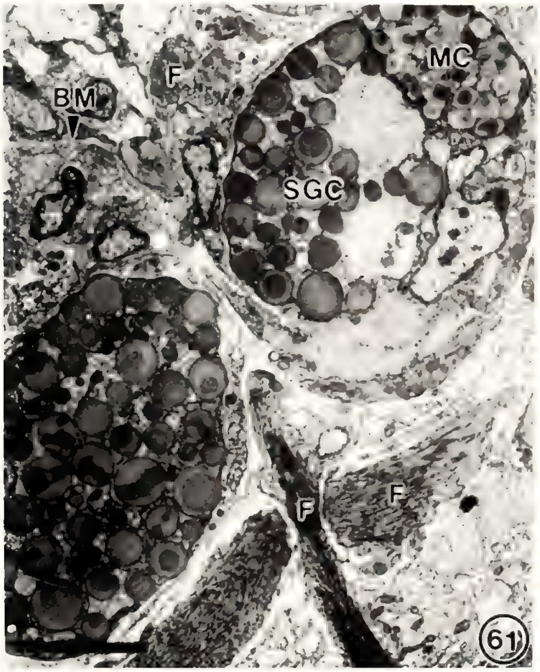
Fig. 53. The periostracum is very thin, and extends across the inner surface of the outer or shell lobe (1G4F, SEM, scale bar = 50 μm). **Fig. 54.** Periostracal groove. The periostracum extends from the gland, across the inner epithelial surface of the outer or shell lobe (0.5 μm, K, MS, scale bar = 20 μm). **Fig. 55.** Inner surface of outer or shell lobe. The surface of most of the epithelial cells is covered by microvilli, although a few cilia are present. The cells are arranged around crypts (1G4F, SEM, scale bar = 10 μm). **Fig. 56.** Inner surface of outer or shell lobe. There are secretory globules at the surface of some of the cells (1G4F, SEM, scale bar = 2.5 μm).











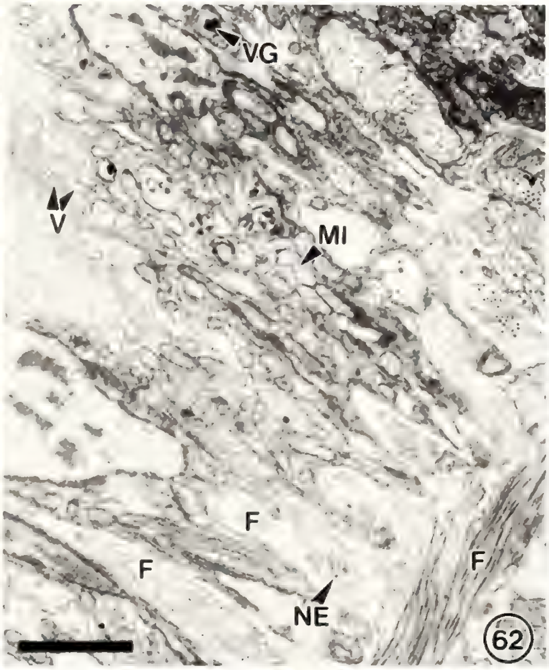
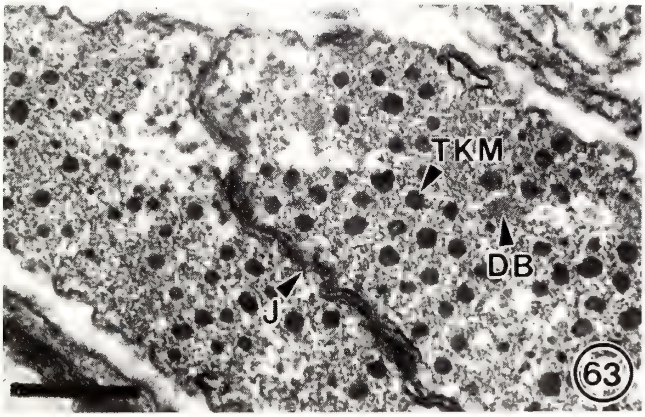


Fig. 57. Muscle fibres from middle lobe, near gland. Thick and thin myofilaments can be distinguished, as well as dense bodies in the centre of the fibre and hemidesmosomes at the sarcolemma. There are vesicles of sarcoplasmic reticulum next to the sarcolemma (K, MS, TEM, scale bar = 1 μm). **Fig. 58.** Muscle fibres from middle lobe, near gland. Transverse and some indication of diagonal banding are seen on the thick myofilaments. A hemidesmosome is present at the sarcolemma (K, MS, TEM, scale bar = 200 nm). **Fig. 59.** Outer lobe, inner surface. The epithelial cells have microvilli at the surface, and there are many vesicles in the apical cytoplasm. They are arranged around crypts filled with secretory material. Many secretory cells containing distinct granules and mucous cells are present. This lobe is contracted, in spite of treatment with magnesium sulphate, so subepithelial muscle fibres are seen in T.S. between the epithelial cells, and in L.S. below this (K, MS, TEM, scale bar = 4 μm). **Fig. 60.** Outer lobe, inner surface, same region as figure 59, showing small epithelial cells around the crypts. These cells contain many apical vesicles, glycogen and mitochondria (K, MS, TEM, scale bar = 2 μm). **Fig. 61.** Outer lobe, inner surface, basement membrane of epithelium at upper left. The bodies of goblet shaped secretory cells are sectioned across below the epithelial surface, and are surrounded by subepithelial muscle fibres. In one case, the bodies of a secretory cell containing distinct granules and a mucous cell appear to be closely associated (K, MS, TEM, scale bar = 4 μm). **Fig. 62.** Outer lobe, outer surface. This epithelium is similar to that of the inner surface, but no goblet shaped secretory cells are present, and there are cell inclusions with dark contents (K, MS, TEM, scale bar = 2 μm).



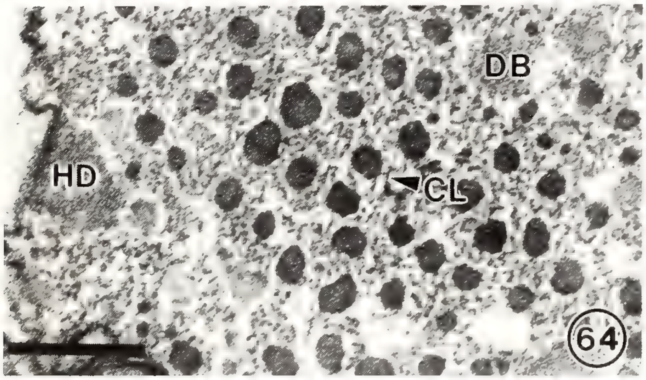


Fig. 63. Outer lobe, inner surface. TS subepithelial muscle fibres. Thick myofilaments, thin myofilaments and dense bodies are present. The sarcolemmas of two adjacent muscle fibres are closely apposed, forming a junction. K, MS, TEM. Scale bar = 300 nm. **Fig 64.** Same region as figure 63. As in the adductor muscle, the thick filaments are wider in diameter the farther away they are from the dense bodies and hemidesmosomes. Cross-links can occasionally be seen between the myofilaments. K, MS, TEM. Scale bar = 200 nm.

equivalent to the ''basal cells'' described in other bivalves, which may be limited to a single row of cells connecting the middle and outer lobes (Wada, 1968; Saleuddin, 1974), or can be two to eight cells deep (Bubel, 1973a). Folding in the periostracum and folds or channels in the apical membrane of the basal cells have been described in the pearl oysters *Pinctada martensii* Dunker and *P. fucata* (Kawakami and Yasuzumi, 1964; Wada, 1968), and other bivalves (Bevelander and Nakahara, 1967; Neff, 1972a; Bubel, 1973a; Saleuddin, 1974); but none have the extensive array of parallel apical cytoplasmic processes described in the periostracal gland of *Crassostrea virginica* in the present account. The cells of this gland need to be studied in more detail.

There is not as abrupt a transition between the cells of the periostracal gland of *Crassostrea virginica* and the epithelial cells of the outer surface of the middle lobe as described in other bivalves, and periostracum appears to be secreted in this transitional region. The glandular region is found in all bivalves, but its extent and number of cell types involved is variable (Saleuddin and Petit, 1983). The periostracal gland is restricted to the base of the groove in *C. virginica* and *Ostrea edulis* Linnaeus, 1750 (Beedham, 1958), where a thin, hyaline periostracum is formed. The latter is entirely organic and nonmineralised in *C. virginica* according to Carriker *et al.* (1980). In other bivalves, the periostracum starts as a thin layer secreted by the basal cells, termed the ''pellicle'' by Beverlander and Nakahara (1967), and becomes thicker and altered in composition as it reaches the free edges of the mantle lobes as a result of secretions by one or both epithelial layers lining the periostracal groove (Beedham, 1958; Beverlander and Nakahara, 1967; Neff, 1972a, b; Saleuddin, 1974; Petit *et al.*, 1979; Saleuddin and Petit, 1983). The epithelial cells of the outer surface of the middle lobe of *C. virginica* contain vesicles and some dense granules. These cells often contain more abundant dense granules in other bivalves (Wada, 1968; Bubel, 1973b; Saleuddin, 1974), but the secretions of these cells do not seem to contribute to the periostracum. In some bivalves the periostracum is closely associated with this epithelium, and it has been suggested that the epithelial cells help to lubricate the periostracum and support it as it moves along the groove (Saleuddin, 1974). Both *C. virginica* and *Pinctada fucata* (Wada, 1968) have ciliated cells in this region, although they are not found in other bivalves (Saleuddin, 1974).

It is generally accepted that the cells lining the inner surface of the outer lobe of bivalves contribute to the periostracum, but crypts have not been described in other bivalves (Beverlander and Nakahara, 1967; Bubel, 1973b). The cells lining the crypts in *Crassostrea virginica* are covered with secretory globules, but the periostracum does not appear to become thicker as it passes along the groove. The crypts of *C. virginica* could result from contraction of the outer lobe, but this would probably result in folds rather than crypts. Goblet shaped secretory cells with bodies extending below the epithelium, like those found in *C. virginica*, have also been described in *Mercenaria mercenaria* (Neff, 1972a), and *Ostrea edulis* (Beedham, 1958). In *O. edulis* these cells were found not to react with stains for mucin, but to be positive for the mercuric bromophenol blue stain for protein. This could contribute to the periostracum. Relatively high concentrations of alkaline phosphatase were found in the epithelium of the inner surface of the outer lobe of *O. edulis* by Beedham (1958). The components required for quinone tanning of the periostracal protein have been found in the periostracum of several bivalves (Saleuddin and Petit, 1983).

The tentacles of the oyster are very extensible, and are sensitive to light, chemicals, suspended particles and temperature according to Galtsoff (1964). The cells with few cilia and dark cytoplasm found near the tips of the tentacles of the middle and inner lobes appear to be connected with the nerve network beneath the epithelium, and are probably simple single-celled receptors, although Galtsoff states that sensory organs are absent. The similar cells found in the pallial epithelium of the mantle could also be receptors, because these occur over the general body surface of other molluscs (Jones and Saleuddin, 1978). Their distribution and structure in *Crassostrea virginica* need to be studied in more detail. They did not appear to be on specialised papillae, like those on the tentacles of the giant scallop *Placopecten magellanicus* (Gmelin) (Moir, 1977); and they seemed to have a variable number of cilia, like those described on the mantle edge of *Helisoma (Planorbella) duryi* Wetherby, 1979 (Jones and Saleuddin, 1978).

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The histology and ultrastructure of the adductor muscle of the eastern oyster *Crassostrea virginica* (Gmelin)

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Abstract. The structure of the translucent and opaque parts of the adductor muscle of the eastern oyster *Crassostrea virginica* (Gmelin) was studied by light and transmission electron microscopy. The muscle was fixed with the valves held closed and after the muscle had relaxed so that the valves gaped. Several fixatives were used, some with recently developed modifications. The muscle fibres of the translucent and opaque parts of the adductor muscle have a similar organisation, with central myofilaments and peripheral sarcoplasmic reticulum, mitochondria and nucleus. In translucent muscle, the thick myofilaments are thinner than they are in opaque muscle, and the dense bodies are sometimes obliquely oriented. Nerve endings and invaginations of the sarcolemma at hemidesmosomes are shown for the first time in oyster adductor muscle. For the first time, presence of paramyosin is indicated by diagonal as well as transverse periodicities in sections of the thick myofilaments of obliquely striated muscle. These muscles are similar to the anterior byssus retractor muscle of the blue mussel *Mytilus edulis* Linné, except that no nexal junctions were found between the muscle fibres.

Larval oysters develop two adductor muscles, the ''dimyarian'' condition, but following attachment the anterior muscle degenerates (Galtsoff, 1964; Elston, 1980), resulting in the ''monomyarian'' condition. Adult bivalves which burrow retain two adductors, which are needed for the movements involved in burrowing; but two adductors are not necessary for the sessile oyster. The single adductor is large and more or less centrally placed, facilitating rapid closing in adverse conditions or when clearing the mantle of detritus. It is made up mainly of translucent muscle, which can contract and close the valves quickly. At one side of the adductor muscle is a smaller, crescent-shaped portion of opaque muscle that contracts more slowly, but can hold the valves shut against the tension of the hinge ligament for several days (Millman, 1964), a phenomenon known as ''catch''.

The gross structure (Galtsoff, 1964; Morrison and Odense, 1973), light microscopy and ultrastructure of the myofilaments and isolated paramyosin filaments of the adductor muscle of the eastern oyster *Crassostrea virginica* (Gmelin) have been described (Philpott *et al.*, 1960; Galtsoff, 1964; Morrison *et al.*, 1970; Cohen *et al.*, 1971; Morrison and Odense, 1974). The most detailed study of the adductor muscle of an oyster is that of the translucent part of the muscle of *Crassostrea angulata* (Lamarck) by Hanson and Lowy (1961). The relationship between thick and thin myofilaments and the structure of isolated thick myofilaments of *C. angulata* has also been studied (Lowy and Hanson, 1962; Elliott, 1964, 1974 and 1979; Hoyle, 1964; Elliott and Lowy, 1970). Bowden (1958) and Salánki and Zs-Nagy (1966) describe the appearance of the muscle fibres in *Ostrea edulis* L. using light microscopy only. Bennett and Elliott (1981) and Elliott and Bennett (1982) show the myofilaments of *O. edulis* in sectioned material, but the other cell organelles were poorly fixed. They also show thick myofilaments isolated from the translucent and opaque parts of the adductor of *O. edulis*, and a striated appearance in tilted cross sections of thick myofilaments from the opaque part. Hanson and Lowy (1960) studied the myofilaments only of an oyster.

These studies were focused on the myofilaments because of the interest in the ''catch'' mechanism. Also, consistently good fixation of the other organelles was difficult to achieve. However, recently modifications of fixatives have been developed which seem to preserve tissues more completely. The present study was undertaken with the expectation that the ultrastructure of the myofilaments and the other organelles could be better preserved, to provide a more complete description of the oyster adductor muscle.

METHODS

Fixatives used were 4% glutaraldehyde in seawater (Morrison, 1970), Karnovsky's fixative (1% glutaraldehyde; 4% formalin prepared from paraformaldehyde, in phosphate buffer; Karnovsky, 1965), 1G4F (1% glutaraldehyde; 4% commercial formalin in phosphate buffer, McDowell, 1978), 1G4F with seawater replacing some of the distilled water (Howard and Smith, 1983), or 2.5% glutaraldehyde in 0.05 M cacodylate buffer (David Sims, pers. comm.). Generally, 1G4F with sea-water added gave better results than with phosphate buffer only, so only micrographs of muscle fixed with the

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former fixative are shown. All solutions were used at pH 7.2.

To obtain fixed preparations of adductor muscles with the valves closed, part of the shell and the tissue around the adductor were removed to permit access of the fixative to the muscle, then the whole oyster was immersed in fixative. To obtain preparations of lengthened adductor muscle, the oyster was placed in 4°C seawater containing 8% $MgSO_4$ (Galtsoff, 1964) or 3.75% $MgCl_2$ (Hanson and Lowy, 1961), which cause the muscle to relax, until the valves gaped. The time taken for this varied from one to several hours, and the gape varied from 1-6 mm. The gape did not appear to alter when the oyster was touched, but to make sure the valves stayed apart dental wax was inserted between the valves. After removing part of the tissue surrounding the adductor muscle to expose the surface, the oyster was placed in fixative. After 1.5 to 2 hours, part of the exposed surface of the adductor muscle fixed at both lengths was removed and small pieces were placed in fresh fixative.

For light microscopy (LM) the specimens were dehydrated in methanol, then embedded in JB4 resin. For transmission electron microscopy (TEM) they were then fixed in 1% osmium tetroxide, dehydrated in acetone then embedded in Taab resin. JB4 resin sections were stained with a 1:50 dilution of 1% toluidine blue in 1% sodium borate, methylene blue/basic fuchsin, or Van Gieson stain (Dougherty, 1981). Taab resin semi-thin sections were also stained with toluidine blue for light microscopy. Sections for electron microscopy were stained with 25% uranyl acetate in methanol (Stempack and Ward, 1964), and lead citrate (Reynolds, 1963), and viewed in an Hitachi transmission electron microscope model MS-9.

Paramyosin paracrystals were prepared from the opaque and translucent part of the adductor, using the method described by Philpott *et al.* (1960) and Johnson *et al.* (1959), who worked on the muscles of several bivalves including *Crassostrea virginica.*

RESULTS

Better general fixation was obtained than in previous studies of oyster muscle. However, results were variable, often within the same section. Areas of poor fixation were sometimes found near the surface as well as deeper in the tissues. 1G4F with seawater was the most dependable fixative. There were periodicities in the thick myofilaments, and details of other cell organelles that were not evident in our earlier studies (Morrison, 1970; Morrison and Odense, 1974).

TRANSLUCENT MUSCLE

The translucent muscle consists of groups of elongate, thin muscle cells or fibres separated by a thin layer of connective tissue, the endomysium (Fig. 1). The elongate nuclei are oriented parallel to the long axis of the muscle cell. The muscle fibres are ribbon-like, so in cross section they appear as flattened ovals about 3-4 μm wide and about 17 μm long, which sometimes bifurcate (Fig. 2). The fibres occur in groups, surrounded by a thicker layer of connective tissue, the perimysium.

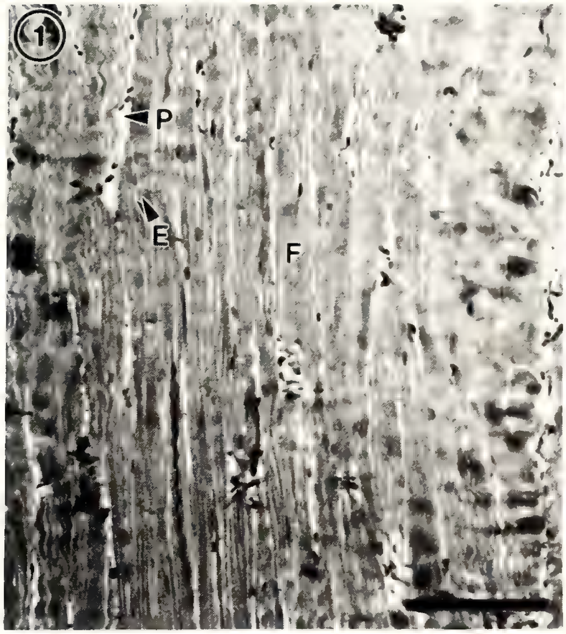
Electron microscopy (Figs. 3, 4) reveals that each muscle fibre is composed of densely packed myofilaments and peripheral mitochondria, sarcoplasmic reticulum and a nucleus. The arrangement of thick and thin myofilaments and dense bodies is usually better shown in muscle which was fixed in an extended condition, after relaxation with $MgSO_4$ or $MgCl_2$ (Fig. 5) than in muscle from oysters fixed with the valves closed. The thin myofilaments are attached to isolated "dense bodies", which are oriented for short distances in oblique bands.

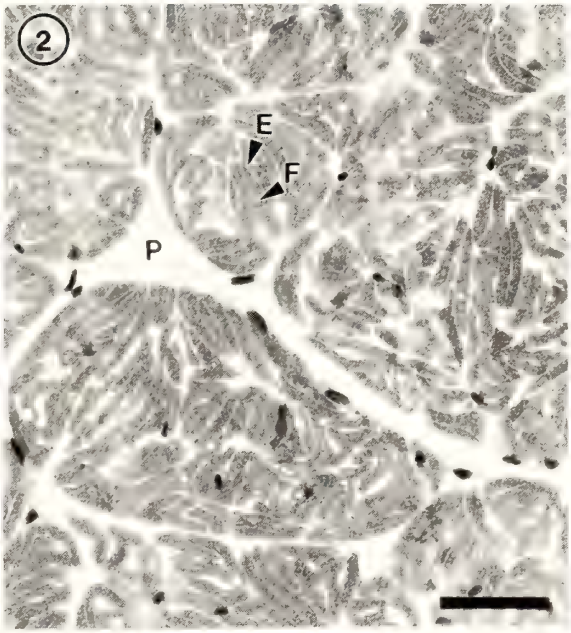
Typically, when viewed with light microscopy no striations are visible (Fig. 1). Oblique striations are occasionally seen, however, in fibres from preparations fixed with the valves closed where the anomalous effect known as "supercontraction" has occurred. The thick myofilaments pass into the regions at the ends of the sarcomeres where there are normally only dense bodies and thin myofilaments, often becoming folded so that obliquely aligned bands are produced, which are visible using light or electron microscopy (Figs. 6, 7).

In a cross section of a sample from an oyster relaxed with magnesium sulphate, fields of thick myofilaments surrounded by thin myofilaments, and of dense bodies among thin myofilaments, can be seen (Fig. 8). The thick myofilaments are regularly arranged in approximate hexagonal arrays.

At higher magnifications the thick myofilaments are cross-striated with a periodicity of about 5 nm. They also have a diagonal periodicity of about 35 nm and sometimes cross-links to adjacent thin filaments have a similar periodicity (Fig. 9). The transverse periodicity also occurs in isolated paracrystals of paramyosin, with every third bar accentuated (Fig. 10). Measurements of 100 thick myofilaments in cross section revealed a modal peak at about 32 nm (range = 18 to 62 nm).

Thin myofilaments are attached to the fusiform dense bodies (Fig. 11). The thick filaments are spindle-shaped, so they appear wider in the centre of a sarcomere and become smaller towards the dense bodies between sarcomeres (Fig. 12). As in mammalian skeletal muscle, where thick and thin filaments overlap the thick myofilaments are surrounded by a ring of thin filaments. This ring is sometimes incomplete around the wider thick myofilaments in the centre of the sarcomere, which would be equivalent to an H zone. Cross links can often be seen between adjacent thick and thin myofilaments and between adjacent thin myofilaments. Some of the dense bodies are attached to the sarcolemma, forming hemidesmosomes (Fig. 13). Filaments from the connective





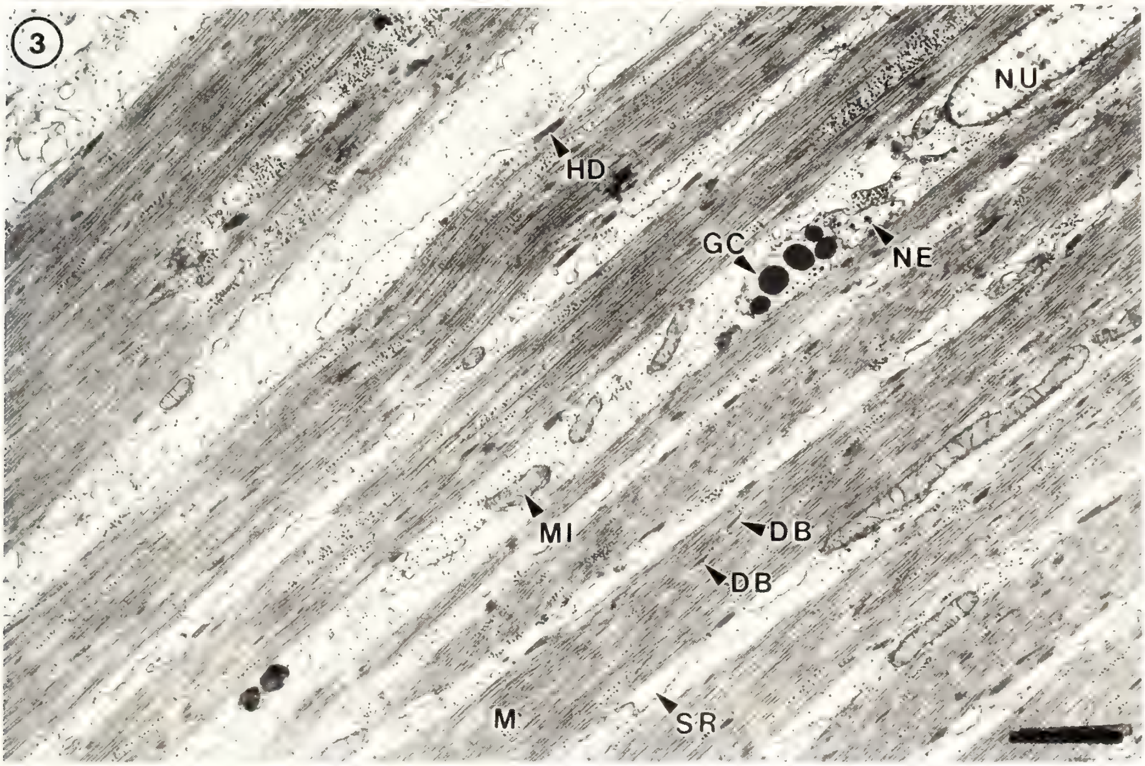
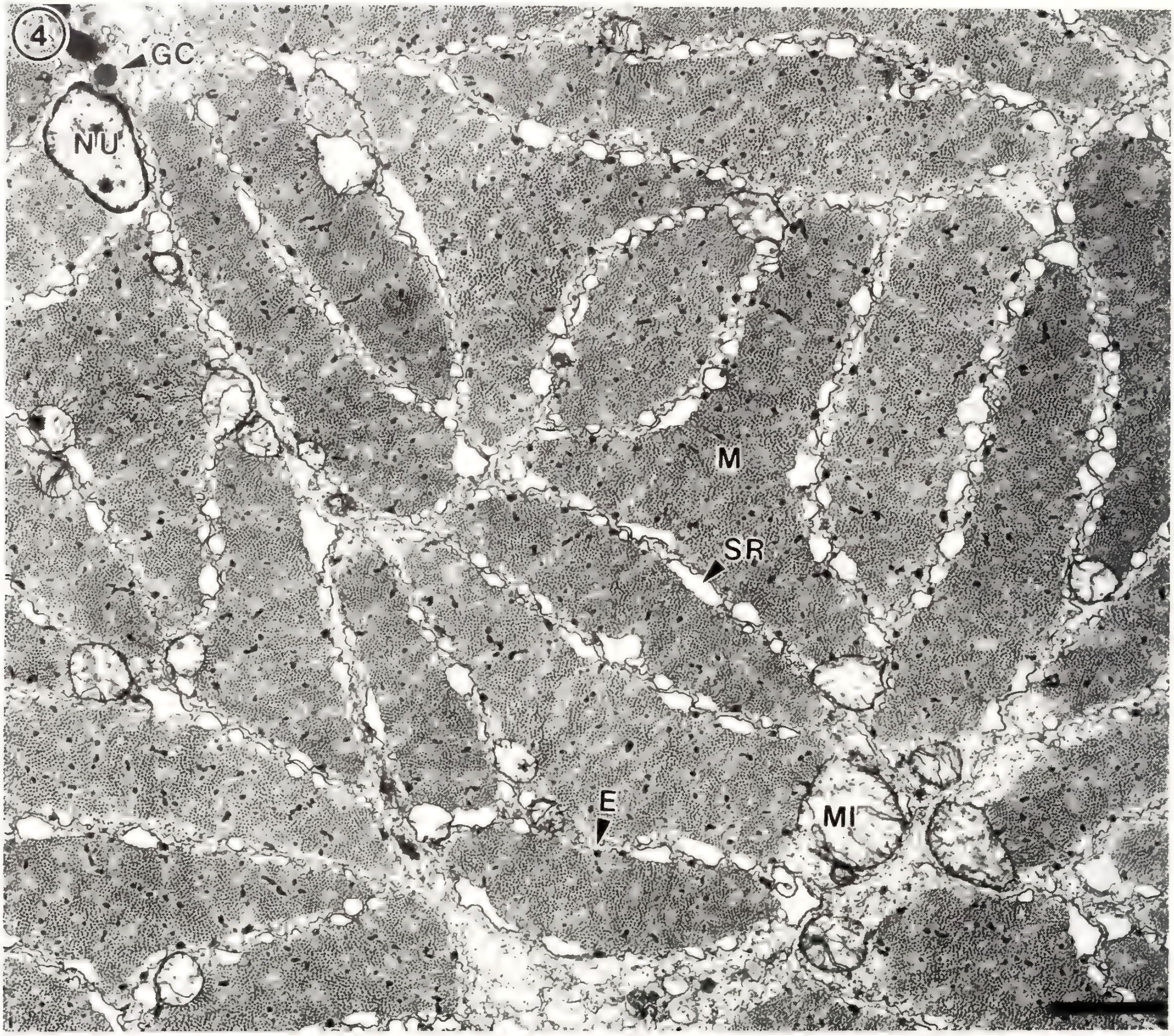


Fig. 1. Longitudinal section (parallel to the muscle fibres of the adductor extending between the two valves of the oyster) of translucent part of adductor muscle. Specimen was fixed in 2.5% glutaraldehyde in caccodylate buffer, embedded in JB4, and stained with toluidine blue. Long, thin muscle fibres (F) are surrounded by endomysium (E), and groups of muscle fibres are surrounded by perimysium (P) (scale bar = 0.1 mm). **Fig. 2.** Cross section (across the adductor muscle) of translucent part of adductor muscle. Specimen was fixed in 2.5% glutaraldehyde in caccodylate buffer, embedded in JB4, and stained with Van Gieson. The profiles of the muscle fibres (F) are elongate and sometimes bifurcate; each fibre is surrounded by endomysium (E), and groups of fibres are surrounded by perimysium (P) (scale bar = 30 μm). **Fig. 3.** Longitudinal section of translucent part of adductor muscle. TEM micrograph of specimen fixed in 1G4F. The muscle fibres have a central core of myofilaments (M) and dense bodies (DB), and hemidesmosomes (HD) are present at the sarcolemma. The peripheral cytoplasm contains elongate mitochondria (MI), sarcoplasmic reticulum (SR) and an elongate nucleus (NU). Between the muscle fibres are glial cells (GC) closely associated with nerve endings (NE) (scale bar = 2 μm).



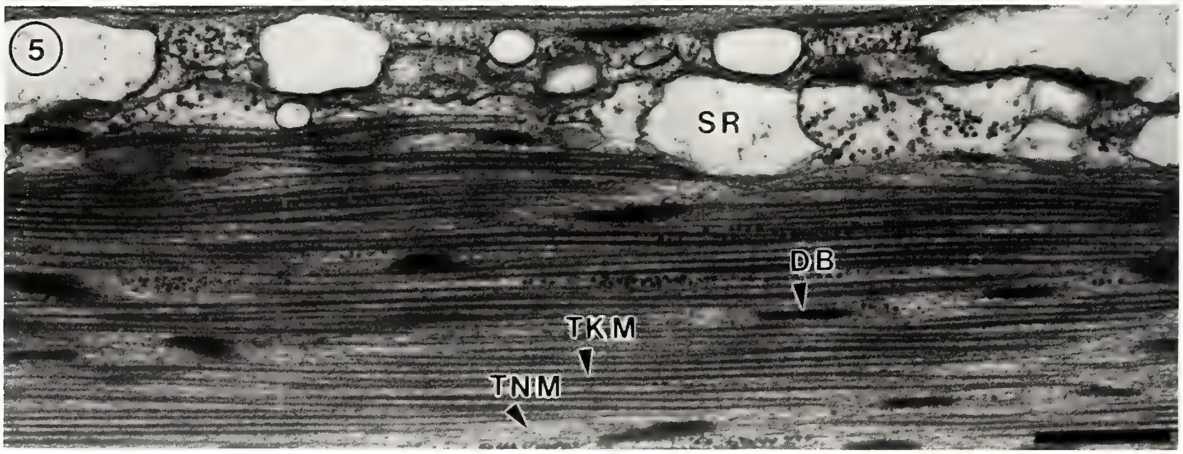
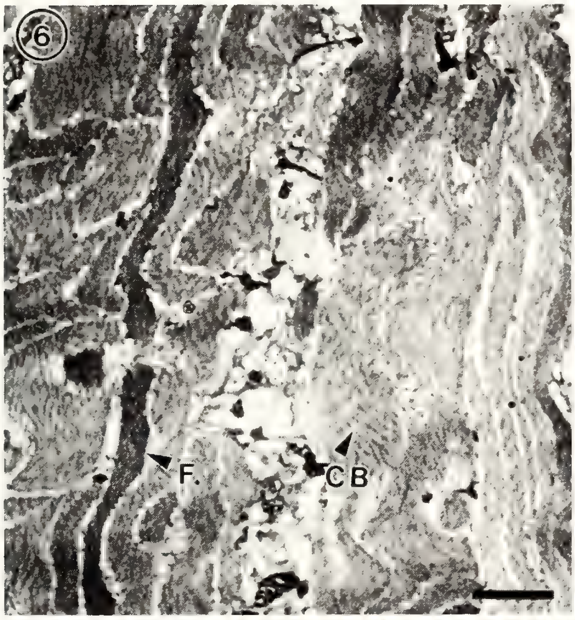
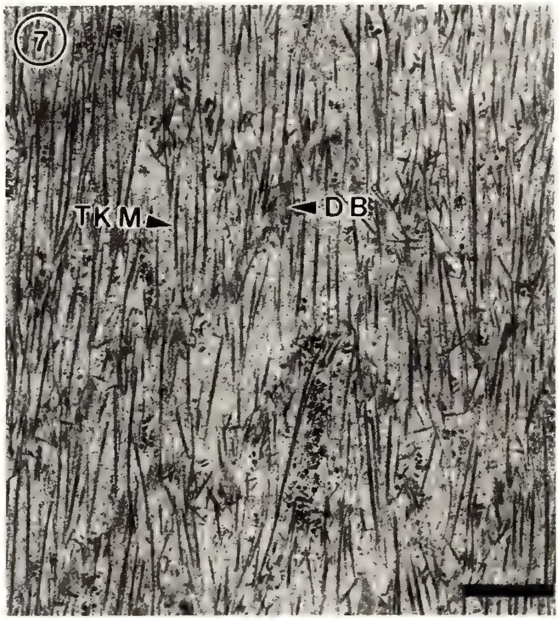


Fig. 4. TEM micrograph of translucent part of adductor muscle of specimen relaxed in Mg SO_4 and fixed in Karnovsky's fixative. The same features can be recognised as in figure 3, but the nucleus (NU), mitochondria (ME) and sarcoplasmic reticulum (SR) are more rounded since this is a cross section [(E) endomysium; (GC) glial cell; (M) myofilaments] (scale bar = 2 μm) **Fig. 5.** TEM micrograph of longitudinal section of muscle fibres of translucent part of adductor muscle. Specimen relaxed in Mg SO_4 and fixed in Karnovsky's fixative. Thick myofilaments (TKM) are present and thin myofilaments (TNM) are continuous with dense bodies (DB), which are obliquely oriented for short distances. There are profiles of sarcoplasmic reticulum (SR) beneath the sarcolemma (scale bar = 1 μm).





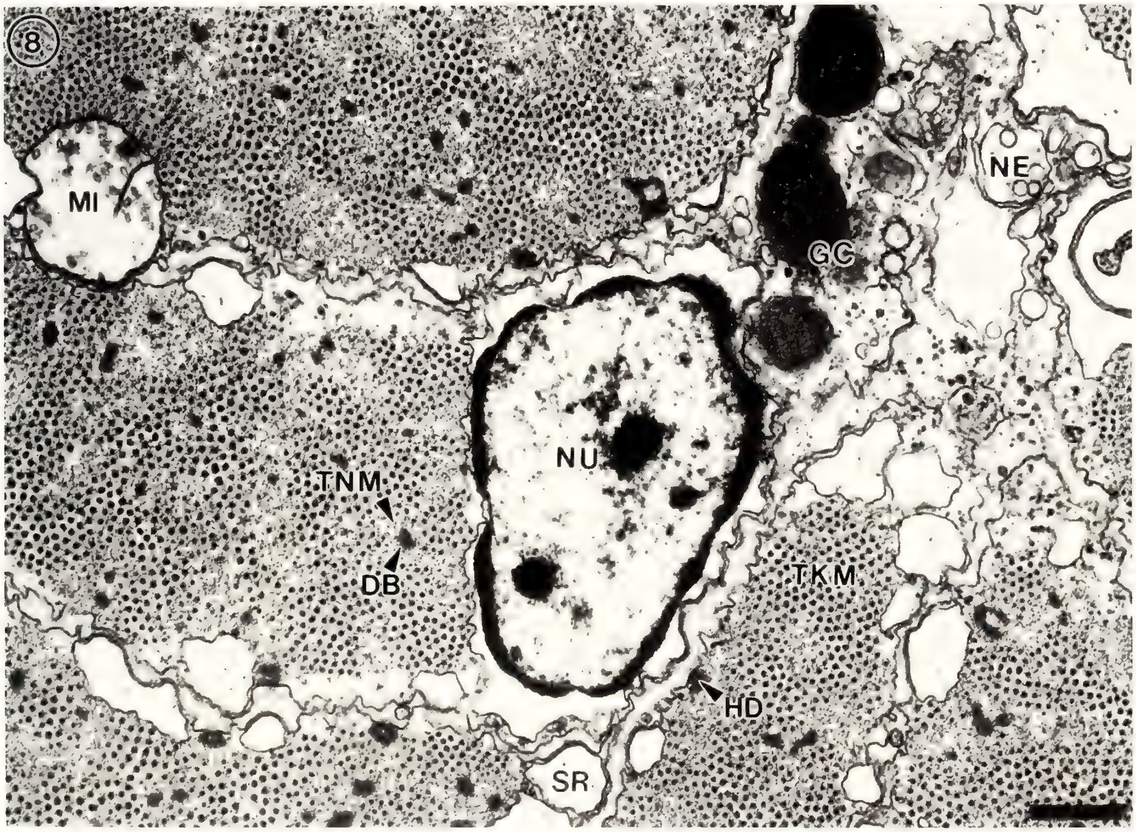


Fig. 6. Longitudinal section of translucent part of contracted adductor muscle of specimen fixed in 2.5% glutaraldehyde in caccodylate buffer and embedded for electron microscopy, 0.5 μm section stained with toluidine blue. Note oblique contraction bands (CB) in the fibres (F) (scale bar = 20 μm). **Fig. 7.** TEM micrograph of longitudinal section of contraction bands of translucent part of contracted adductor muscle. Specimen fixed in 2.5% glutaraldehyde in caccodylate buffer. Thick myofilaments (TKM) overlap and become folded in regions where there are dense bodies (DB) (scale bar = 1 μm). **Fig. 8.** TEM micrograph of cross section of translucent part of adductor muscle. Specimen relaxed in Mg SO_4 and fixed in Karnovsky's fixative. There are fields of thick and thin myofilaments (TKM) and thin myofilaments (TNM) in the muscle fibres, and dense bodies (DB) occur in the fields of thin myofilaments. Hemidesmosomes (HD) present at the sarcolemma. The nucleus (NU) is rounded in cross-section. Vesicles of sarcoplasmic reticulum (SR) as well as mitochondria (MI) occur beneath the sarcolemma. A glial cell (GC) with an accompanying nerve ending (NE) is present between the muscle cells (scale bar = 500 nm).

tissue stroma accumulate next to the hemidesmosome. The sarcolemma is often invaginated where there are hemidesmosomes (Figs. 3, 8).

The profiles of sarcoplasmic reticulum are situated just beneath the sarcolemma, and dense material can be seen between the outer membrane of the sarcoplasmic reticulum and the sarcolemma (Fig. 14). The sarcolemmas of adjacent muscle cells are often close to each other (Figs. 3-5, 8), but no well-defined junctions were seen. Many of the mitochondria in one specimen have filamentous paracrystals and annulated cristae (Fig. 15).

Nerve endings, which contain a variety of vesicles, some small and clear, some dense-cored or of varying density, often occur close to the sarcolemma (Figs. 3, 16). Glial cells containing large granules, the gliosomes, are usually closely associated with these nerve endings but do not completely surround them.

OPAQUE MUSCLE

The muscle fibres of the opaque muscle are more rounded in cross section than those of translucent muscle, so their diameter (10-20 μm) is similar to that of the length but larger than the width of the oval profiles of the translucent muscle fibres (Figs. 17, 18). In the transitional zone between the translucent and opaque muscle the muscle fibres of each type are intermingled (Fig. 19). As in the translucent muscle, each muscle fibre is surrounded by endomysium, and the groups of fibres by perimysium. The arrangement of cell organelles is also similar. Central myofilaments are surrounded by vesicles of sarcoplasmic reticulum and mitochondria, and the sarcolemmas of neighbouring cells are often closely opposed (Figs. 20, 21). The nucleus is situated in cytoplasm to one side of the cell, oriented with its long axis parallel with that of the muscle cell, and dense material can be seen between the sarcolemma and the sarcoplasmic reticulum (Fig. 22).

The thick myofilaments are thicker than those of the translucent muscle, having a modal peak at about 61 nm (range = 18 to 123 nm). They exhibit cross striations at 5 nm and often diagonal striations like those of translucent muscle, but they are more evident (Figs. 23, 24). Every third cross striation is accentuated. Cross links occur between the thick and thin myofilaments (Figs. 25, 26), and some thin myofilaments have cross links to more than one thick myofilament (Fig. 25). As in the thick myofilaments of the translucent muscle fibres, the cross links seem to have a similar periodicity to that of the diagonal bands.

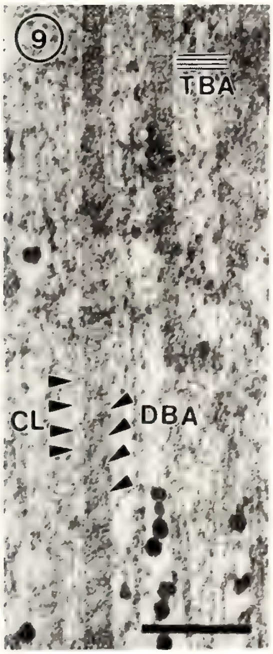
Sometimes, there is a single ring of thin myofilaments surrounding each thick myofilament in the region of overlap, but more often there are several thin myofilaments between the thick myofilaments. Cross links can sometimes be seen between adjacent thin myofilaments, and occasionally connections can also be seen between thick myofilaments (Fig. 26). When the thick myofilaments are cut obliquely, they often appear to be banded (Fig. 27).

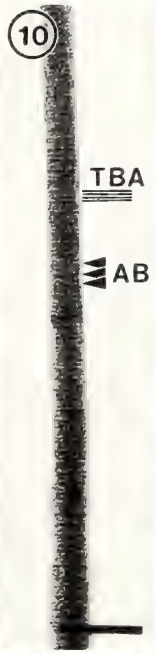
The thin filaments are attached to dense bodies (Fig. 28) which do not show any special arrangement in the muscle fibre (Fig. 29), so this type of muscle is classified as smooth. As in the translucent muscle fibre, some dense bodies are attached to the sarcolemma, forming hemidesmosomes (Fig. 30), and filaments of connective tissue in the endomysium are closely associated with the sarcolemma at these sites. In some places the sarcoplasm surrounding the myofilaments is wide, and sarcolemmal invaginations containing filaments of connective tissue extend to the hemidesmosomes (Fig. 31). Glial cells and axons occur between the muscle fibres. Nerve endings, often accompanied by glial cells, are found next to the sarcolemma, sometimes embedded in the sarcoplasm (Fig. 32). They contain a variety of small clear and dense-cored vesicles and larger vesicles containing a varying amount of dense material.

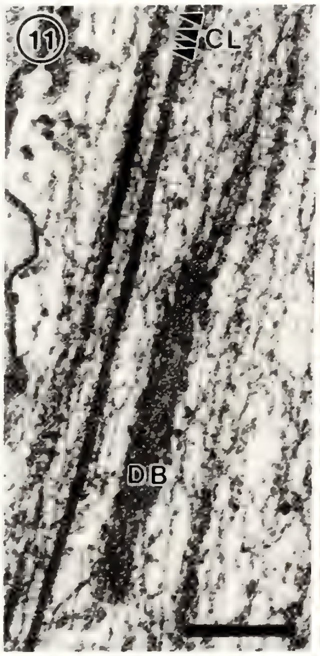
DISCUSSION

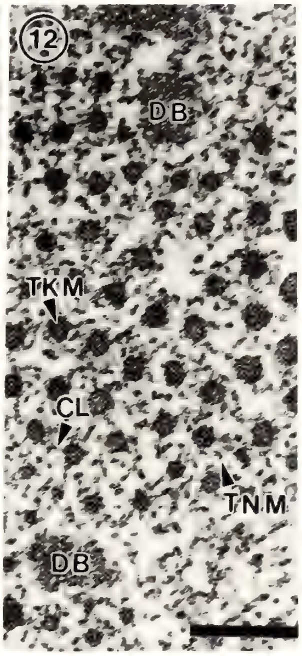
The adductor muscle of oysters, as in most bivalved molluscs, consists of uninucleate muscle cells of small diameter (3-20 μm) that are much longer than those of vertebrate smooth muscle (Twarog, 1976). Each muscle cell contain a single myofibril, and peripheral vesicles of sarcoplasmic reticulum which form couplings with the sarcolemma, as described in the adductor muscle of the scallop, *Argopecten irradians* (Lamarck, 1819) (Nunzi and Franzini-Armstrong, 1981) and the translucent part of the adductor muscle of *Crassostrea angulata* (Hanson and Lowy, 1961). The invaginations of the sarcolemma at the hemidesmosomes are not as well defined as the transverse tubular system of transversely striated muscle or some unstriated muscle (Dorsett and Roberts, 1980), but may perform a similar transport function.

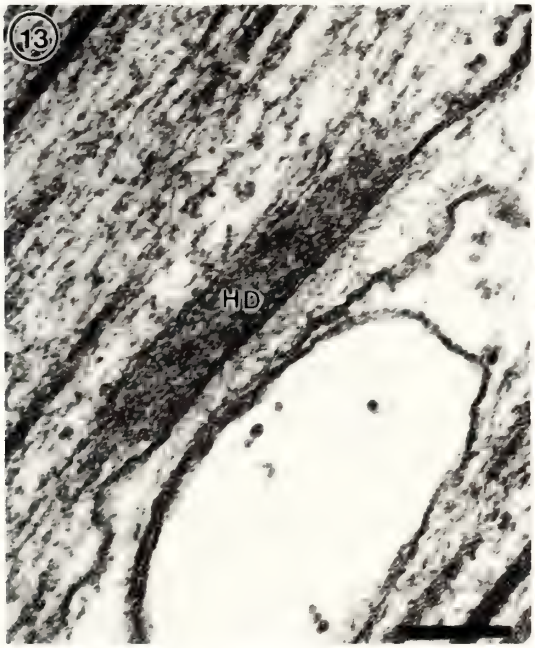
The dense bodies, like the Z-line of striated muscles, anchor the actin filaments. In the translucent part of the adductor of *Crassostrea virginica* they form oblique bands as in *C. angulata*, in which the bands are arranged helically around the outer part of the fibre and branch and anastomose in the centre of the muscle fibre (Hanson and Lowy, 1961). These bands were not seen in normal muscle in this study, but can be seen using phase contrast illumination (Hanson and Lowy, 1961). The contraction bands of supercontracted muscle are obvious using regular as well as phase illumination (Bowden, 1958; Hanson and Lowy, 1961; Galtsoff, 1964; Salánki and Zs-Nagy, 1966; Morrison and Odense, 1974). More regular oblique banding occurs in some molluscs such as the octopus and cuttlefish, where the myofibrils surround a central core of mitochondria (Millman, 1967). In this study, the dense bodies, and the actin filaments entering them, were easier to see in specimens fixed in 4% glutaraldehyde in sea











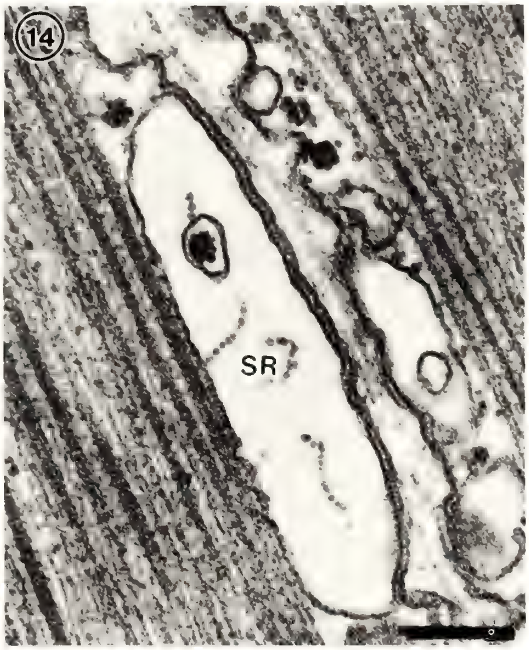
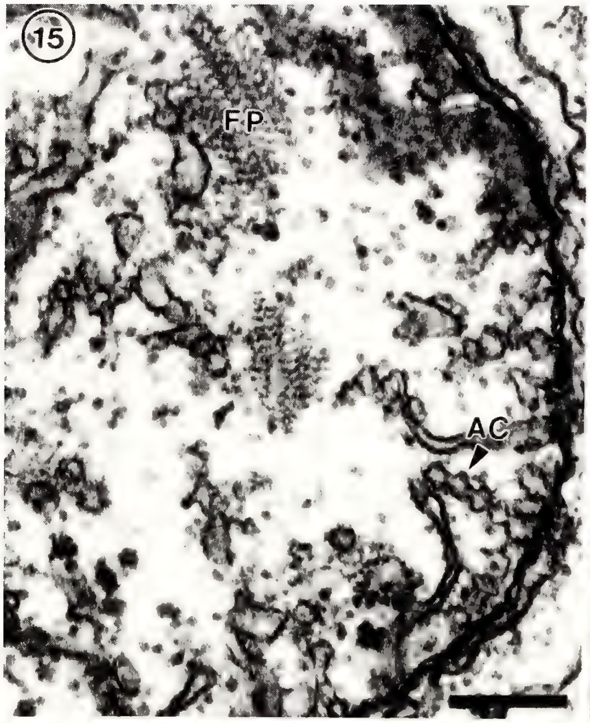
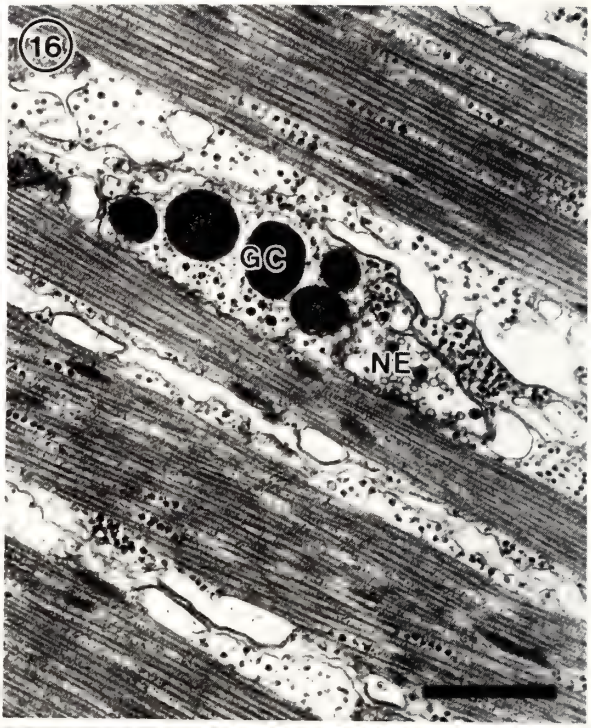
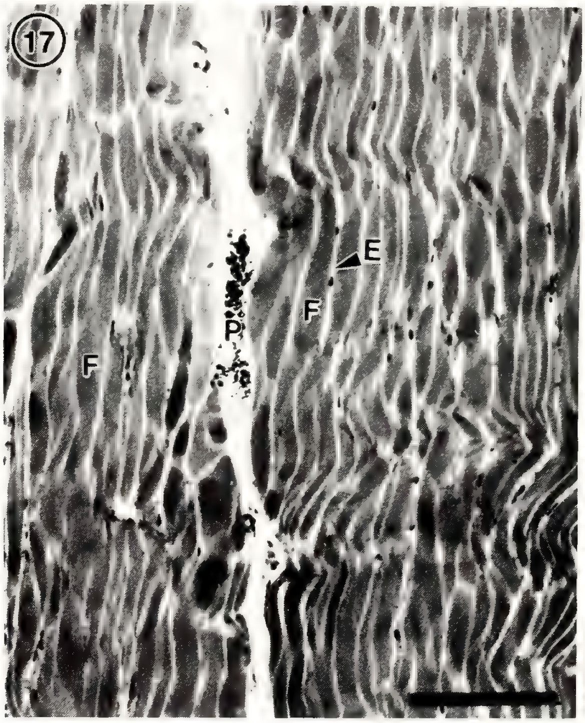


Fig. 9. TEM micrograph of longitudinal section of translucent part of adductor muscle of specimen fixed in 2.5% glutaraldehyde in caccodylate buffer. The thick myofilaments exhibit transverse banding (TBA) at intervals of about 15 nm and diagonal banding (DBA). Cross-links (CL) to the actin filaments can be seen in some areas, at about the same intervals as the diagonal banding (scale bar = 100 nm). **Fig. 10.** Translucent part of adductor muscle showing paramyosin paracrystal with narrow transverse bands (TBA) about 5 nm apart and accentuated bands (AB) about 15 nm apart (scale bar = 10 nm). **Fig. 11.** TEM micrograph of longitudinal section of translucent part of adductor muscle of specimen relaxed in Mg SO_4 and fixed in Karnovsky's fixative. Cross links (CL) occur between the thick and thin myofilaments, as well as between the thin filaments. The latter enter dense bodies (DB) (scale bar = 200 nm). **Fig. 12.** TEM micrograph of cross section of translucent part of adductor muscle of specimen relaxed in Mg SO_4 and fixed in Karnovsky's fixative. Thick myofilaments (TKM), thin myofilaments (TNM) and dense bodies (DB) are present. Each thick myofilament is surrounded by a ring of thin myofilaments, and cross-links (CL) can often be seen between the two types of myofilament (scale bar = 100 nm). **Fig. 13.** TEM micrograph of longitudinal section of translucent part of adductor muscle of specimen relaxed in Mg SO_4 and fixed in Karnovsky's fixative. There is a hemidesmosome (HD) to one side of the double membrane forming the sarcolemma; on the other side there are connective tissue filaments (scale bar = 200 nm). **Fig. 14.** TEM micrograph of longitudinal section of translucent part of adductor muscle of specimen fixed in 1G4F. A thin layer of dense material is present between a vesicle of sarcoplasmic reticulum (SR) and the sarcolemma (scale bar = 200 nm).







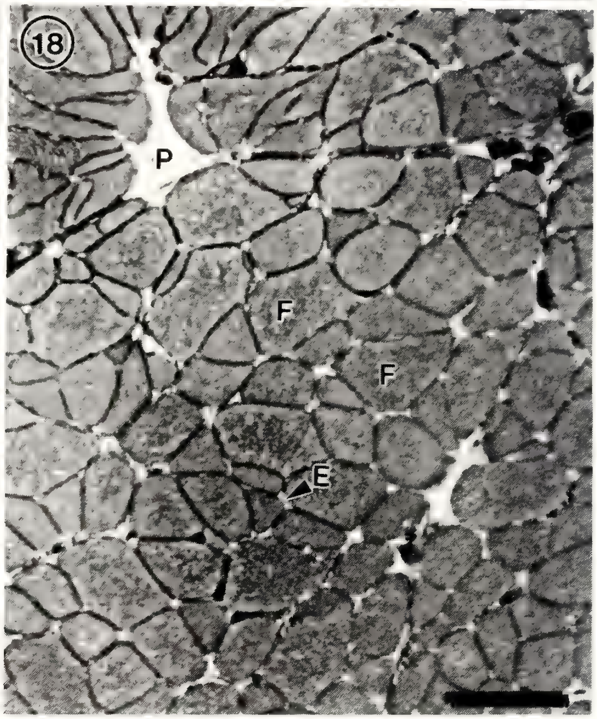


Fig. 15. TEM micrograph of transverse section of translucent part of adductor muscle of specimen relaxed in Mg SO_4 and fixed in Karnovsky's fixative. A mitochondrion contains filamentous paracrystals (FP) and annulated cristae (AC) (scale bar = 200 nm). **Fig. 16.** TEM micrograph of longitudinal section of translucent part of adductor muscle of specimen fixed in 1G4F. There is a nerve-ending (NE) containing clear and dense vesicles, and an associated glial cell (GC) near the sarcolemma (scale bar = 1 μm). **Fig. 17.** Longitudinal section of opaque part of adductor muscle of specimen fixed in 2.5% glutaraldehyde in caccodylate buffer, embedded in JB4 and stained with toluidine blue. The muscle fibres (F) that are wider than those of the translucent muscle, and are separated by endomysium (E) and perimysium (P) (scale bar = 0.1 mm). **Fig 18.** Cross section of opaque part of adductor muscle of specimen fixed in 2.5% glutaraldehyde in caccodylate buffer, embedded in JB4 and stained with methylene blue/basic fuschin. The muscle fibres (F) are large and have a rounded profile [(E) endomysium; (P) perimysium] (scale bar = 20 μm).

water used in earlier work than in more recently developed fixatives, presumably because less background material in the cell was fixed.

Dense bodies also form hemidesmosomes at the sarcolemma in the anterior byssus retractor muscle (ABRM), where it has been suggested that they give structural stability to the muscle by attaching the muscle cells to the closely associated filaments of connective tissue (Twarog, 1967; Twarog *et al.*, 1973) and propagate tension to neighboring cells via the collagen of the connective tissue (Sobieszek, 1973; Twarog, 1976). Hanson and Lowy (1961) suggested, in their study on the translucent adductor muscle of *Crassostrea angulata*, that the sarcolemma may be interrupted next to the dense body, but it can be clearly seen that this is not the case in the present study (Fig. 13).

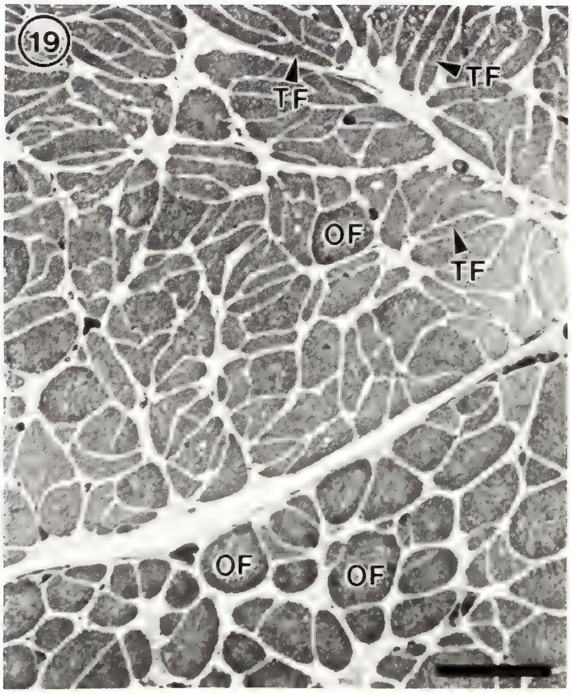
In the ABRM nexal or gap junctions about 15 nm across which may be sites of intercellular conductivity have been described between the muscle cells (Twarog *et al.*, 1973), but these were not seen in the present study. However, the sarcolemmas of adjacent cells often run parallel to each other farther apart, but over greater distances than those found in nexal junctions. This has been reported in several other molluscs (Zs.-Nagy and Salánki, 1970; Nicaise and Amsellem, 1983).

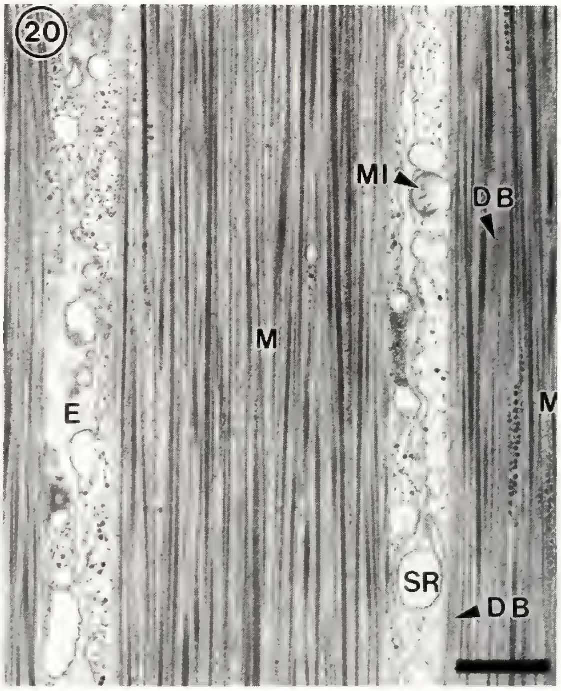
The filamentous paracrystals found in the mitochondria of one specimen are similar to those described in the mitochondria of the myocardial cells of *Crassostrea virginica* (Hawkins *et al.*, 1980). These workers also found prismatic cristae, and our specimen had annulated cristae. Their specimens, like ours, appeared to be otherwise normal, although in other animals paracrystals are usually associated with disease or states of altered metabolism.

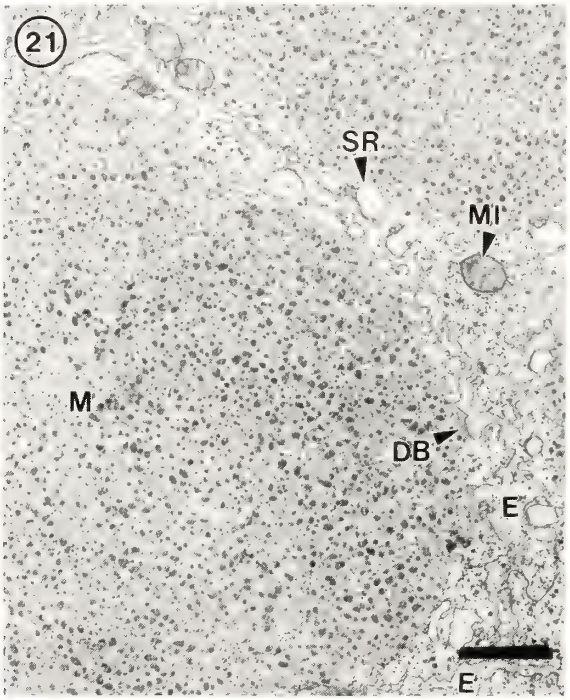
Glial cells like those found in both the translucent and opaque parts of the adductor muscle in this study have been described forming a "glio-interstitial network" between tonic muscle cells in a variety of molluscs, including the tonic muscle of the adductor of *Anodonta*, and the ABRM of *Mytilus edulis* (Amsellem *et al.*, 1973; Gilloteaux, 1975; Nicaise and Amsellem, 1983). They have not previously been recorded in phasic muscles. These authors suggest that these cells may help to control metabolic exchanges between the interstitial spaces and the nerves and/or muscles.

The opaque muscle tissue of the adductor examined in this study is very similar in appearance and physiology to the ABRM of the mussel (Lowy and Hanson, 1962; Millman, 1964; Twarog, 1967; Heumann and Zebe, 1968; and Sobieszek, 1973). However, its thick myofilaments are wider than those of the ABRM, which have a peak width of about 40 nm (Sobieszek, 1973). Unlike the translucent muscle, there is no obvious arrangement of dense bodies. Lowy and Hanson (1962) assert that some degree of order is necessary for the sliding-filament mechanism to work efficiently, and such an order has been demonstrated in the ABRM using optical diffraction techniques (Sobieszek, 1973). Sobieszek postulates that there are sarcomeres consisting of three to four thick myofilaments which are 25 μm long, thin myofilaments which are 140 μm long and two dense body halves. Such sarcomeres would be difficult to recognise in sectioned material, since they are so long and narrow, so they may be present in the opaque adductor muscle of *Crassostrea virginica*. Cross-bridges between the thick and thin myofilaments have been shown in other mollusc muscle cells, such as those of the ABRM, in varying degrees of contraction. It has been suggested that direct interaction occurs between the thick myofilaments (Hoyle, 1983), as indicated by the close relationship sometimes seen between them (Fig. 26); but other workers believe that this does not play a part in contraction (Bennett and Elliot, 1989).

The thick myofilaments of vertebrate striated muscle are very constant in diameter (about 16 nm) and length (about 1.6 μm); whereas the thick myofilaments of most mollusc fibres, including those described in the present study, are wider and vary in width (Levine *et al.*, 1976). This is associated with the presence of varying amounts of paramyosin (Millman, 1967). The proportion of paramyosin in transversely striated muscles such as the fast part of the adductor of *Placopecten magellanicus* (Gmelin) is low (7% by mass; Chantler, 1991), but is higher in obliquely striated muscle such as that of the translucent part of the adductor of *Crassostrea angulata* (16-20%; Chantler, 1983) and highest in smooth muscle such as that of the opaque part of the adductor of *C. angulata* (22-39%; Chantler, 1983). Paramyosin forms the core of the thick myofilament, surrounded by myosin (Szent-Györgyi *et al.*, 1971) and gives a typical X-ray diffraction pattern originally described by Bear (1944) and Bear and Selby (1956), which subsequently became known as the Bear-Selby net. The transverse striations with a periodicity of about 15 nm, and diagonal striations with a periodicity of about 35 nm described in the thick myofilaments of the translucent and opaque muscle in this study form a "checkerboard" pattern characteristic of the paramyosin core of "catch" muscle (Hanson and Lowy, 1964; Chantler, 1991). The diagonal striations have not been shown previously in a translucent or phasic muscle. These periodicities were first shown by Hall *et al.* (1945) to correspond to the pattern formed by the Bear-Selby net, and result from the tendency of paramyosin molecules to assemble with a 14.5 nm intermolecular shift as a result of intermolecular ionic interactions (Kendrick-Jones *et al.*, 1969; Castellani and Cohen, 1987). The relationship between the patterns seen in paramyosin and myofilament preparations from "catch" muscle using the electron microscope and the Bear-Selby net are considered in detail by Elliott and Lowy (1970), Cohen *et al.* (1971), and Elliott (1979). The banding patterns seen in thick myofilaments in oblique sections of the opaque muscle in the present study (Fig. 27) have also been







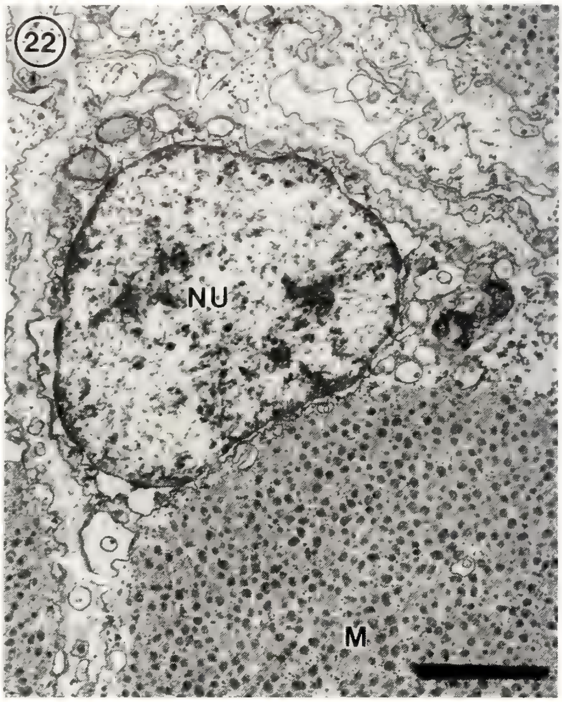
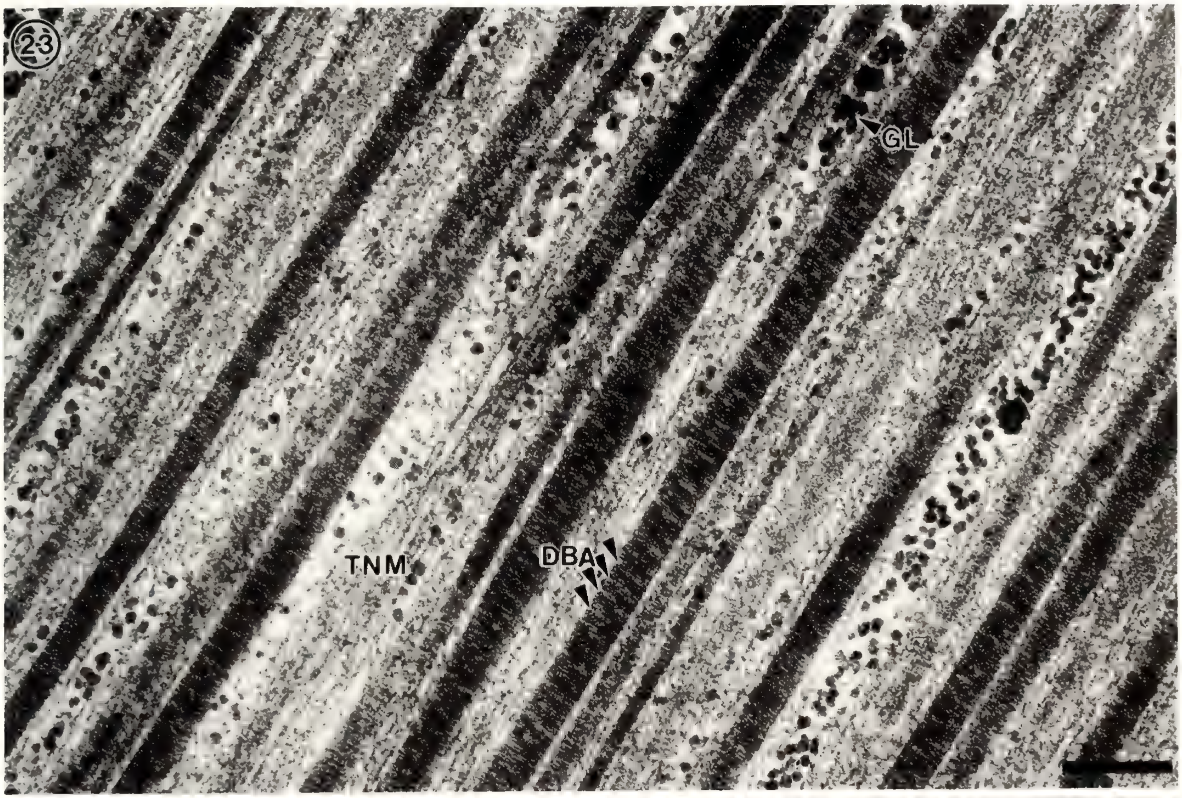
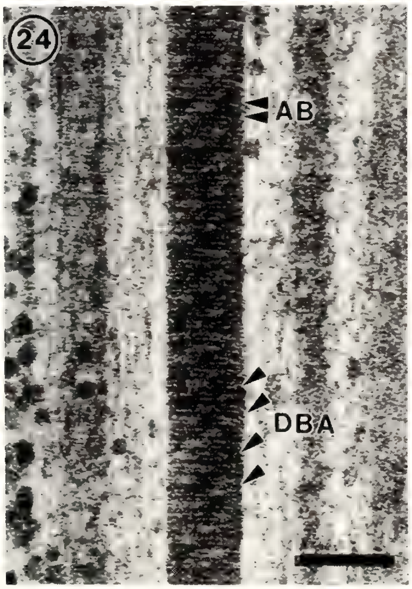
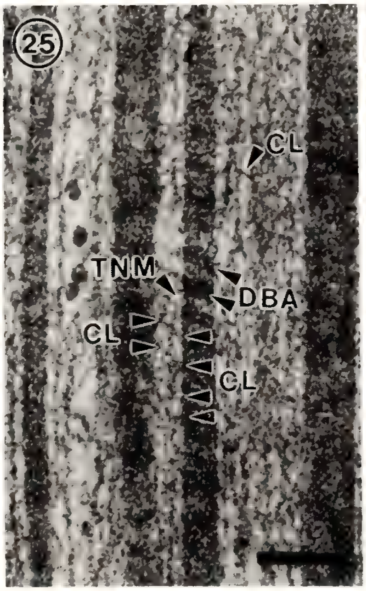


Fig. 19. Transverse section of the transition zone between the opaque and translucent parts of the adductor muscle of specimen fixed in 2.5% glutaraldehyde in caccodylate buffer, embedded in JB4 and stained with methylene blue-basic fuschin. Thick opaque fibres (OF) can be seen to the bottom of the micrograph, and more elongate, thinner translucent ones (TF) can be seen to the top. In the centre fibres of both types are intermingled (scale bar = 20 μm). **Fig. 20.** TEM micrograph of longitudinal section of opaque part of adductor muscle of specimen relaxed in Mg Cl_2 and fixed in 2.5% glutaraldehyde in caccodylate buffer. A central core of myofilaments (M) and dense bodies (DB) is present in each muscle fibre. There are mitochondria (MI) and vesicles of sarcoplasmic reticulum (SR) next to the sarcolemma. These are not as elongate as in translucent muscle. Endomysium (E) is present between muscle fibres (scale bar = 1 μm). **Fig. 21.** TEM micrograph of cross section of opaque part of adductor muscle of specimen fixed in Karnovsky's fixative, showing the dense bodies (D), endomysium (E), myofilaments (M), mitochondria (MI) and sarcoplasmic reticulum (SR) seen in longitudinal section in figure 20 (scale bar = 1 μm). **Fig. 22.** TEM micrograph of cross section of opaque part of adductor muscle fixed in Karnovsky's fixative. The nucleus (NU) appears rounded, and is in the cytoplasm to one side of the myofilaments (M) (scale bar = 1 μm).







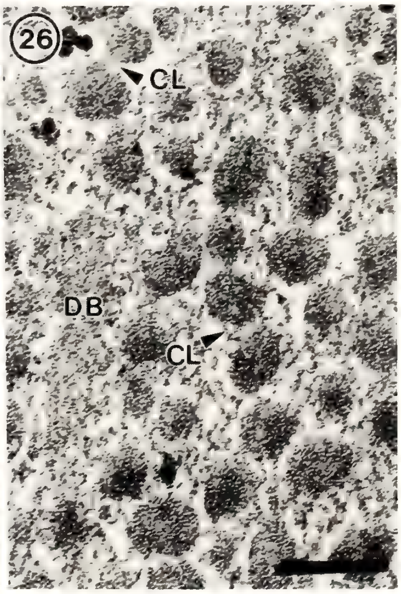
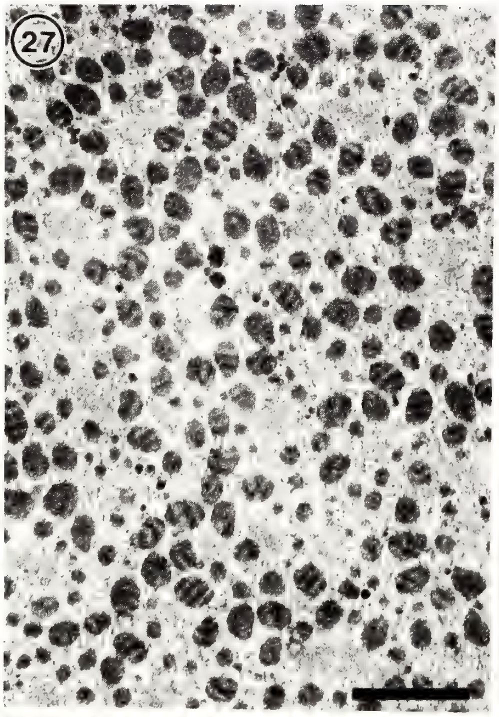
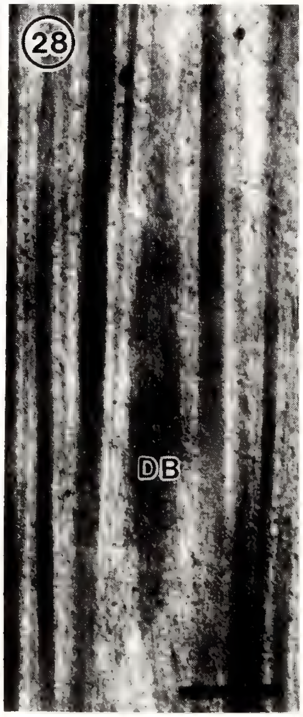
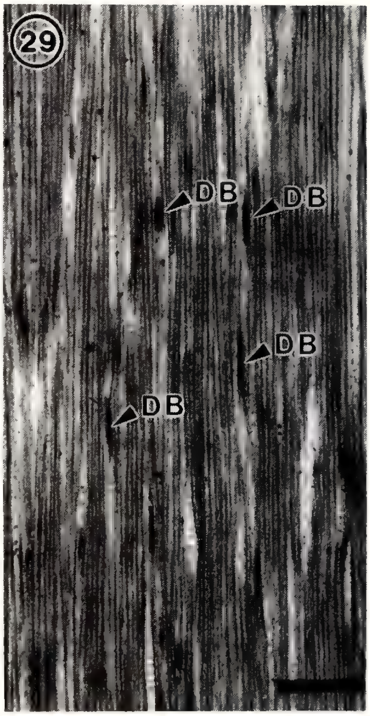
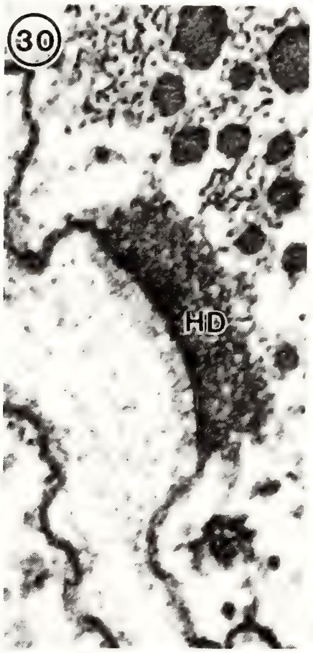


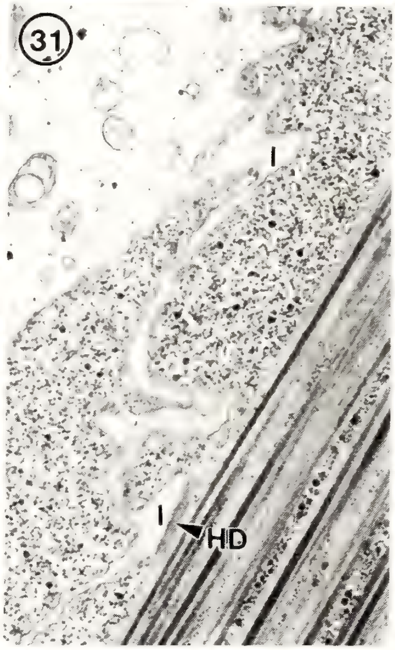
Fig. 23. TEM micrograph of longitudinal section of opaque part of adductor muscle of specimen fixed in 2.5% glutaraidehyde in caccodylate buffer. The thick myofilaments have transverse and diagonal banding (DBA), and sometimes seem to be very close together. Thin filaments (TNM) and glycogen (GL) can also be seen (scale bar = 200 nm). **Fig. 24.** TEM micrograph of longitudinal section of opaque part of adductor muscle of specimen fixed in 2.5% glutaraldehyde in caccodylate buffer. Transverse banding can be seen, with every third band accentuated (AB). Diagonal banding (DBA) is also present (scale bar = 100 nm). **Fig. 25.** TEM micrograph of longitudinal section of opaque part of adductor muscle of specimen fixed in Karnovsky's fixative. There are cross-links (CL) between thick and thin myofilaments, and also between thin myofilaments. CL have a similar periodicity to the diagonal bands (DBA) on the thick myofilaments. One thin myofilament (TNM) has links to two thick myofilaments (scale bar = 100 nm). **Fig. 26.** TEM micrograph of cross section of opaque part of adductor muscle of specimen relaxed in Mg Cl_2 and fixed in 2.5% glutaraldehyde in caccodylate buffer. Cross-links (CL) are present between thick and thin myofilaments, and also occasionally between thick myofilaments. A dense body (DB) can be distinguished (scale bar = 100 nm).











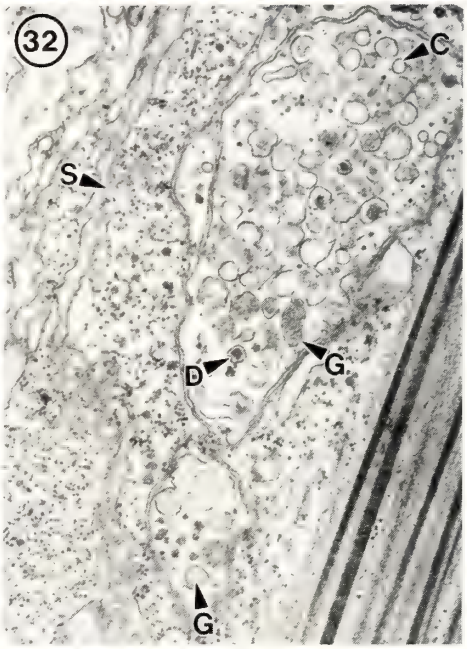


Fig. 27. TEM micrograph of cross section of opaque part of adductor muscle of specimen relaxed in Mg Cl_2 and fixed in 2.5% glutaraldehyde in caccodylate buffer. Light and dark bands cross the thick myofilaments (scale bar = 300 nm). **Fig. 28.** TEM micrograph of longitudinal section of opaque part of adductor muscle fixed in 4% glutaraldehyde in seawater. Thin actin myofilaments enter the dense body (DB) (scale bar = 300 nm). **Fig. 29.** TEM micrograph of longitudinal section of opaque part of adductor muscle of specimen fixed in 4% glutaraldehyde in seawater. There is no definite pattern in the distribution of the dense bodies (DB) (scale bar = 1 μm). **Fig. 30.** TEM micrograph of cross section of opaque part of adductor muscle of specimen relaxed in Mg SO_4 and fixed in Karnovsky's fixative. The sarcolemma is invaginated next to a hemidesmosome (HD), and connective tissue filaments are concentrated in the adjacent endomysium (scale bar = 100 nm). **Fig. 31.** TEM micrograph of longitudinal section of opaque part of adductor muscle of specimen fixed in Karnovsky's fixative. A long invagination of the sarcolemma extends to a hemidesmosome (HD) at the sarcolemma (scale bar = 1 μm). **Fig. 32.** TEM micrograph of longitudinal section of opaque part of adductor muscle of specimen fixed in 2.5% glutaraldehyde in caccodylate buffer. Nerve endings are embedded in the sarcoplasm and contain small clear (C) and dense-cored vesicles (D) as well as vesicles with varying amounts of granular contents (G), which are usually larger than the other types. An invagination (I) of the sarcolemma (S) extends to the myofibril (scale bar = 500 nm).

shown in *Ostrea edulis, C. angulata, C. gigas* Thunberg, 1793, *Mercenaria mercenaria* (Linné, 1758), *Pecten maximus* (Linné, 1758) and the ABRM of *Mytilus edulis* when cross sectioned material was tilted (Bennett and Elliott, 1981; Elliott and Bennett, 1982), and these authors show that these patterns are caused by viewing the myofilaments down planes of the Bear-Selby net.

The thin myofilaments of the sea scallop adductor muscle have been shown to be very similar to those in vertebrates (Chantler, 1991). The thin myofilaments of the oyster have a similar appearance and diameter, suggesting that they also have a similar composition. In the translucent adductor muscle, there appear to be about 12 thin myofilaments around each thick myofilament, as reported in *Crassostrea angulata* (Hanson and Lowy, 1961).

The muscle fibres of the opaque part of the adductor of *Placopecten magellanicus* (Cohen *et al.*, 1971) sometimes have obliquely aligned dense bodies, and the thick myofilaments have a similar peak diameter, 36 nm (Morrison and Odense, 1974) as those of the obliquely striated, translucent muscle of the oyster. They contain paramyosin and exhibit a small degree of "catch" (Hoyle, 1964). The obliquely striated muscle of the oyster also has some ability to maintain "catch" (Hanson and Lowy, 1961), and its X-ray pattern shows the Bear-Selby net typical of paramyosin (Elliott and Bennett, 1982). The presence of paramyosin is also demonstrated by the transverse and diagonal periodicities found in sectioned material in the present study. These two types of muscle are therefore very similar, although one forms the opaque, slow part and the other the fast, translucent part of an adductor muscle.

Smooth and obliquely striated muscles in the adductors of bivalves have the same arrangement of organelles, and in this study their thick myofilaments show the same banding patterns. There appears to be a spectrum of muscle cell types in bivalve adductor muscles, with slightly varying ultrastructural characteristics, the latter producing a graded series of physiological characteristics.

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The Asiatic clam *Corbicula fluminea* (Müller, 1774) (Bivalvia: Corbiculidae) in Europe

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Abstract. Two populations of *Corbicula fluminea* were found in the Iberian Peninsula; one in Spain and the other in Portugal. A detailed description in terms of ecology, shell morphology and microstructure, morphometrics and anatomy is given for the Spanish population from the Miño River. Lectotypes for *Tellina fluminea* and *T. fluminalis*, and a neotype for *T. fluviatilis* are designated and illustrated. Distribution and spread of *C. fluminea* in Europe are revised. Comparisons among some European populations and the populations from Canton, China, and the Miño River are made. Results suggest that, except for one doubtful population, all records of *Corbicula* in Europe are attributable to *C. fluminea.*

Corbicula taxonomy begins in 1774 with Müller who described three species in the genus *Tellina* Linné, 1758: *T. fluminalis* "in fluvio Asiae Euphrat"; *T. fluminea* "in arena fluviali Chinae"; *T. fluviatilis* "in flumine emporium Canton Chinae praeterlabente". Since then, many living species of *Corbicula* Mühlfeldt, 1811, have been described in freshwater and estuarine habitats from Southeast Asia, the Indian subcontinent, the Pacific islands, and the easternmost part of Europe and Africa (McMahon, 1983). The fossil record of *Corbicula* includes Europe, North America and Japan (see Linstow, 1922; Zhadin, 1952; Ellis, 1978; and Britton and Morton, 1979 for a review).

The first published record of *Corbicula* in North America is that of Burch (1944) in 1938. Counts (1981, 1985) cites the presence of the species in 1924 and 1937 in Nanaimo, Vancouver Island, British Columbia, Canada, and in Raymond, Pacific County, Washington, respectively. Since then, it spread widely in most lotic and lentic habitats, being a pest with very important economic and ecological effects (Sinclair and Isom, 1963; McMahon, 1983). Many papers have been published with records of new localities and biological data using different species names, mainly *C. fluminea, C. manilensis* and *C. leana* (McMahon, 1983 and references therein). Several hypotheses about the importance of the role of human activities in the spread of *Corbicula* have been treated (e.g. Thompson and Sparks, 1977; McMahon, 1982).

The wide geographical and ecological range of *Corbicula* seems to be related to the great variation in shell form and colour. These two features are the most common taxonomic characters and the only ones used by the early conchologists, suggesting that *Corbicula* taxonomy probably involves more species names than needed.

Thus, Talavera and Faustino (1933) (*In:* Britton and Morton, 1979) placed *Corbicula manilensis* (Philippi, 1844) into synonymy with *C. fluminea*, Morton (1977) considered *C. leana* to be a junior synonym of *C. fluminea,* while *C. fluviatilis* was previously placed into synonymy with *C. fluminea* by Prashad (1929). Moreover, a thorough review by Britton and Morton (1979) lead the authors to consider that most Asiatic species previously described could be attributed to two taxa: the freshwater species *C. fluminea* (Müller, 1774) and the estuarine species *C. fluminalis* (Müller, 1774).

Studying North American populations of *Corbicula* on the basis of ecology, functional morphology and reproductive biology, Britton and Morton (1979) concluded that all belonged to the single species, *C. fluminea.* The results of this paper, and the conclusions of Morton (1982), seem to provide a good discrimination between *C. fluminea* and *C. fluminalis.*

In the last decade, *Corbicula* was also introduced into South America (Ituarte, 1981) and Europe. Mouthon (1981) reports the presence of *C. fluminalis* in France (La Dordogne) and in Portugal (Tajo River estuary). Nagel (1989) cites the species from the Duero River near Oporto (Portugal) and Girardi (1989-1990) indicates the occurrence of *C. fluminalis* also in France at the Canal du Midi at Grisolles (Tarn and Garonne). We found two *Corbicula* populations in the Iberian Peninsula, one in Spain and the other in Portugal, apparently corresponding to *C. fluminea.* These facts suggest that, as occurred in North America, Europe is being currently invaded by this bivalve and that species discrimination is probably not as clear as previously thought (Morton, 1982), because it still seems to allow the use of various species names for morphological variants of the same species concept.

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Thus, the Iberian populations are described in detail in relation to shell and anatomical characters in order to clarify the taxonomy and distribution of *Corbicula*. The results are compared with bibliographical data and museums material, including the Müller collection.

MATERIALS AND METHODS

The Miño River was sampled from its source to its mouth. The first samplings were carried out in July and October 1989. From June 1990 to June 1991 a monthly sampling was done at Goian, near Vigo in Galicia, Spain, 13 kms from the sea (Fig. 1) (UTM coordinates 29TNG208436).

The specimens of the Duero River were collected at Regua (Portugal) in the shore by the Karaman-Chappuis method (Motas, 1962). In the Miño River, the clams were collected by snorkeling, dredging the bottom and sieving the mud along the shore.

Temperature, dissolved oxygen, pH and water turbidity were monitored at Goian (Miño River) using an Horiba water checker Model U-7. Conductivity was measured using a Crison conductivimeter Model 523. Values of alkalinity, calcium, total water hardness and carbonate hardness were obtained *in situ* with Merck Aquamerck. No physicochemical data are available from the Duero River.

Some specimens were maintained alive in aquaria at the laboratory for anatomical studies. Prior to the dissections, animals were relaxed with menthol or 1% sodium-pentobarbital (nembutal), extracted from the valves and stained with neutral red.

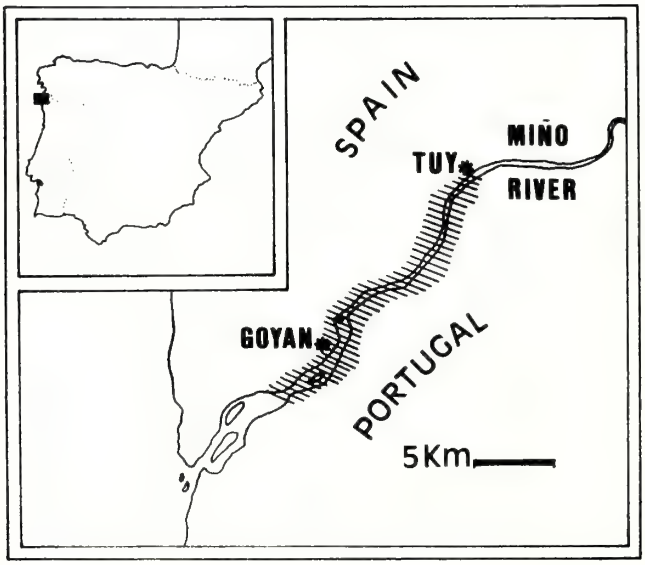

Fig. 1. Map of the distribution of *Corbicula fluminea* in the Miño River.

Shell pores and other microstructural features were observed in the Miño River population with a Jeol JSM T330A scanning electron microscope at accelerating voltages of 15 and 20 kV. Juvenile and adult valves were submerged in 5% sodium hypochlorite (Clorox) for more than 24 hours, cleaned in distilled water with ultrasound, dried at 50°C and then coated (whole or fractured) with a thin layer of gold-palladium in a Balzer SCD 004 Sputter Coating Unit.

Shell phenotypes were described. Then, the specimens were compared with descriptions in the literature and specimens in the collections. In addition to the typical measures (length, width and height), and to describe the variability of *Corbicula* shells, seven measurements shown in figure 2C plus the shell perimeter were determined using a caliper read to the nearest 0.01 mm and *camera lucida* drawings of each left valve. The total shell length (L) was used as a standard size measure for statistical adjustment of the measured variables. The angle (A) inscribed between the inner inflection point of the hinge and the ends of the lateral teeth, and the one between the lines d and d′ in figure 2C (Add′) were also measured on the *camera lucida* drawings, and transformed in radians for statistical analysis. We also registered the number of sulcations per 5 mm medially measured along the dorsoventral axis and the number of denticles per millimeter in the anterior lateral tooth, both in the left valve. A total of 58 European specimens of *Corbicula* were measured: 45 from the Miño River at Goian (Spain), nine from the Duero River at Regua (Portugal) and four from the Duero (Portugal) (Karl Otto-Nagel, coll.).

The mean, standard error, standard deviation and the coefficients of variation from the Miño River population were calculated to evaluate the least variable characters and therefore the most suitable for taxonomic purposes. The Müller collection material listed in the following section was also measured for comparisons. These were made among Miño, Duero (Regua), Duero (Nagel coll.) and Canton populations.

Corbicula lacks well-defined stages of growth and adult size is highly variable. In addition, sampling biases due to the use of previously collected material from archival collections could cause artificial heterogeneity across samples (Reist, 1985). Thus for morphometrics to be useful for taxonomy they must compensate for allometric relationships and be able to estimate differences in shape by removing confounding effects of absolute shell size. As size and shape covary, an analysis of covariance, with L as the covariate (Packard and Boardman, 1987), was performed on the original data and the among-groups residuals used to describe shape and in subsequent statistical procedures (Reist, 1985, 1986). The residuals of each measurement were then examined by an analysis of variance and Duncan multiple range test to determine significantly different pairs of means.

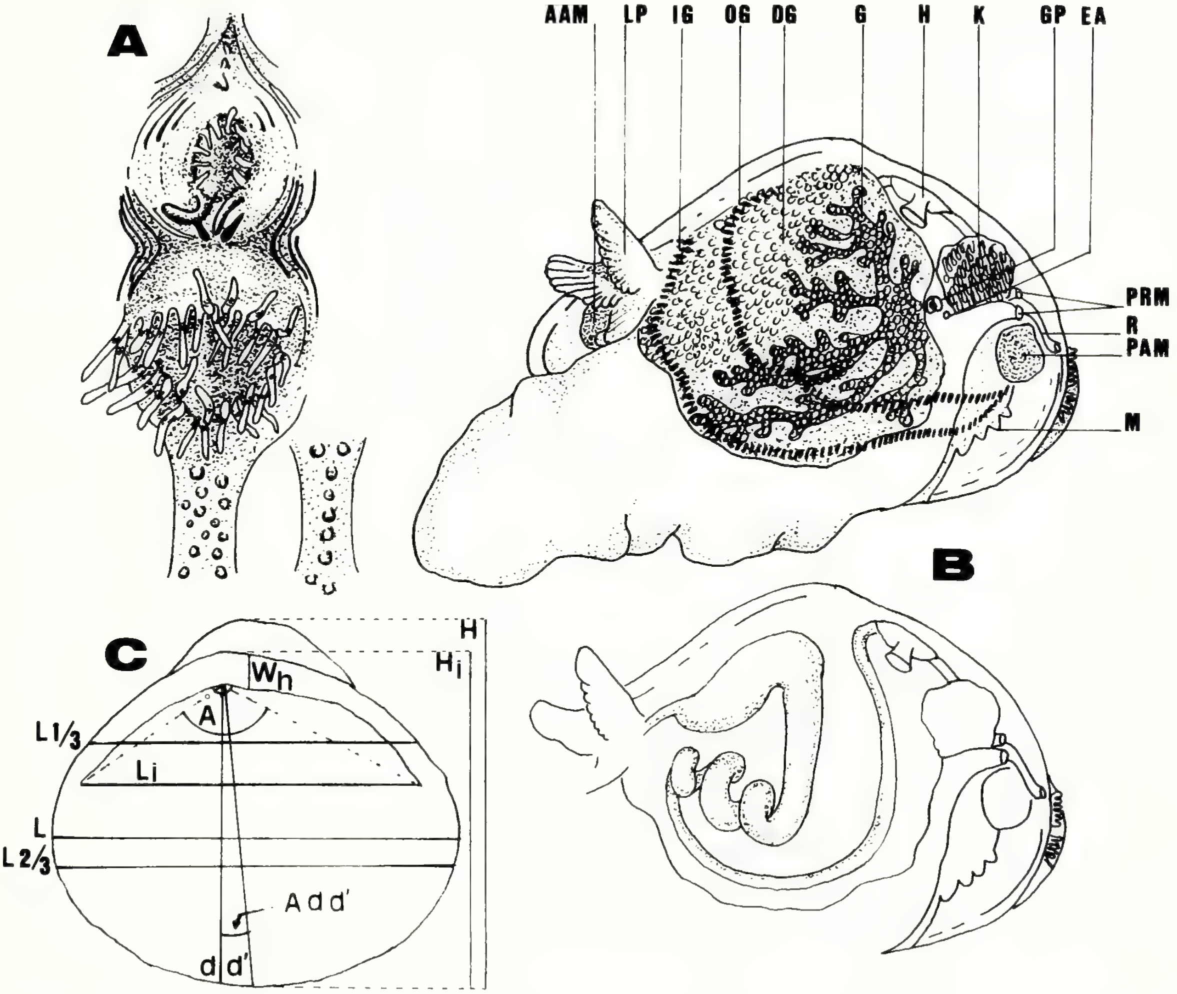

Fig. 2. Spanish *Corbicula fluminea:* **A,** siphons; **B,** anatomy (AAM, anterior adductor muscle; LP, labial palps; IG, inner gill; OG, outer gill; DG, digestive gland; G, gonad; H, heart; K, kidney; GP, gonopore; EA, excretory aperture; PRM, posterior pedal retractor muscle; R, rectum; PAM, posterior adductor muscle, M, mantle). **C,** left valve showing standard measurements (L, length; L ⅓, length at ⅓ of height; L ⅔, the same at ⅔; Li, length between the ends of the lateral teeth; H, height of the shell; Hi, distance between the upper border of the hinge and the lower end of the shell; W, width of the complete shell; Wh, width of the hinge; P, perimeter of the valve; d, distance between the angle down the anterior cardinal tooth and the lower end of the valve, perpendicular to Li; d′, bisector of the mentioned angle; A, angle; Add, angle between d and d′.

TYPE MATERIAL

Concerning the three species of *Corbicula* described by Müller (1774), it was impossible for us to find any properly designated type material. Counts (1991) says that the holotypes of *Corbicula fluminea, C. fluminalis* and *C. fluviatilis* are in the Universitetets Zoologisk Museum of Copenhagen (UZMC), and Morton (1977) and Britton and Morton (1979) illustrate three of these specimens as the types of the three species. However, no data about the origin of the supposed type specimens of *C. fluminea* and *C. fluviatilis* are available at the Zoologiske Museum (T. Schiøtte, pers. comm.). On the other hand, it was impossible to obtain specimen #152926 of *C. fluminea* in the Museum of Comparative Zoology at Harvard cited as the paratype by Counts (1991) and quoted by Johnson (1959) as cotype. Therefore, in this paper we designate lectotypes for *Tellina fluminea* and *T. fluminalis* and a neotype for *T. fluviatilis* as follows.

Tellina fluminea. There is no type designated properly. We have studied the following material from the UZMC: two whole shells and two valves from an unknown locality in Müller's collection; three whole shells and two valves from Canton, China, unknown collection; 15 whole shells from Canton, China in Spengler's collection; one whole shell from Canton, China. Probably in Müller's collection (T. Schiøtte, pers. comm.). This specimen was quoted and figured without label data by Kennard and Woodward (1926) as the "cotype" (meaning syntype). It is designed here as the lectotype; one whole shell from East India or China in Müller's collection. It was quoted and figured by Prashad (1929) who stated that it could be accepted as the "cotype" of the species. This specimen was figured by Morton (1977) and Britton and Morton (1979) and taken to be the type. It is not recognized here as a syntype because of the doubtful locality and because its measurements do not fit the original description. **Lectotype** (Fig. 3): The specimen (14.9 x 13.7 x 10.2 mm) from Canton, China, and probably in Müller's collection (UZMC) agrees with the original description and measurements (Müller, 1774).

Tellina fluminalis. The mention of a "cotype" from Müller's collection by Kennard and Woodward (1926) is not a valid lectotype designation. We consider that the mention of "type" by Britton and Morton (1979: Fig. 3) is a valid designation of lectotype according to the Article 74 a of the ICZN. **Lectotype:** (Fig. 3). One specimen (29.9 x 30 x 21.8 mm) from the Euphrates River, Mesopotamy, in Müller's collection (UZMC) agrees with the original description, measurements and locality (Müller, 1774).

Tellina fluviatilis. Kennard and Woodward's (1926) plesiotypes have no nomenclatural value, not coming from Müller's specimens. Prashad (1929) recorded one specimen as the topotype. This is not a valid designation. The specimen figured by Morton (1977) and Britton and Morton (1979) is from Spengler's collection. The sole specimen of this species in Müller's collection is from Tranquebar, India, therefore we designate here the specimen from Canton, China, figured by Morton (1977) and Britton and Morton (1979) as the neotype of the species. **Neotype:** One specimen (19.6 x 17 x 10.6 mm) from Canton, China, in Spengler's collection (UZMC) agrees with the original description and locality. The specimen is equivalve, near equilateral and integropaleate, with an external sculpture of concentric sulcations. There are eight sulcations in 5 mm of the medial region of the left valve. The colour of the periostracum is dark brown with a pale medial concentric band. The umbones are eroded and white. Internally it is violet, darker near the edge and in the area of the siphons. Lateral teeth are white with eight denticles per millimeter measured in the medial region of the anterior lateral tooth of the left valve (Fig. 3). The left valve shows the manuscript letters "Sp".

RESULTS

ECOLOGY

No *Corbicula* were observed in the samples collected in July 1989. Nine juvenile specimens were found in October 1989, and in June 1990 a large number of adults and juveniles were found. Several samplings since then show that the number of *Corbicula* and the area occupied are increasing. In January 1991 the species reached from 8 to 24 km upstream (Fig. 1). The population found at Regua (Portugal) in April 1989 indicates that the species also invaded the Duero River where it lives buried into the gravel in the margins of the river.

In the Miño River, *Corbicula* lives in a section of river 400 m wide that is under tidal influences. Water temperature ranges from 9.2°C in January to 27°C in July. Accordingly, registered values of pH are from 5.9 to 8.2. Values of conductivity at 25°C are low as expected from freshwater habitats in granitic areas. Minimum value is 54 μs which correspond to January. It increases during the summer reaching to 450 μs in September. These values are clearly associated with those of total hardness (1 - 3.8 °dH) for the same months. Less variation was found for carbonate hardness (1 - 1.8 °dH). Calcium varies from 7 to 18 mg/l and alkalinity from 0.4 to 0.8 mmol/l. Higher values of both parameters were also registered in summer. These yearly variations seem to be related with changes in the marine influence and the water river contribution. The Miño River has well oxygenated waters as shown by the observed values of dissolved oxygen, between 7.8 and 12.4 ppm.

Specimens in the shore were sampled at a depth up to 8 cm, which means that at low tide *Corbicula* lives some hours out of the water. Many more specimens were observed living in the middle of the river (about 6 m depth) in gravel and sandy substrata, than in the sand and mud of the shore. They are also frequent in the mud retained by the vegetation. Flora of the area includes many *Elodea canadensis* Michx., an invasive species, *Potamogeton* sp., *Ranunculus* sp. and *Ceratophyllum* sp.

Other molluscs living in the area are: *Musculium lacustre* (Müller, 1774); *Pisidium amnicum* (Müller, 1774); *P. henslowanum* (Sheppard, 1823); *Potomida littoralis* (Cuvier, 1797); *Unio pictorum* (Linné, 1758); *Anodonta cygnea* (Linné, 1758); *Gyraulus* sp.; *Bithynia tentaculata* (Linné, 1758); *Potamopyrgus jenkinsi* (Smith, 1889); *Valvata piscinalis* (Müller, 1774); *Lymnaea* sp.; *Hippeutis complanatus* (Linné, 1758); *Physa acuta* Draparnaud, 1805 and *Ancylus* sp. The abundance of *Bithynia tentaculata* was spectacular. It is also important to mention that *Pisidium amnicum* was one of the dominant molluscan species in the samples prior to September 1990. In this month only a few specimens were found and since then the population has become extinct. This was coincident with the appearance of a pest of the Cyanophyta *Microcystis aeruginosa* (Kütz). However, in spite of the fact that the algal bloom receded, in the following month no living specimens of *P. amnicum* could be found. In the most downstream locality for *Corbicula* the only accompanying species was *P. jenkinsi* whose abundance is considerable.

SHELL MORPHOLOGY AND MICROSTRUCTURE

The shell of European *Corbicula* is equivalve, near

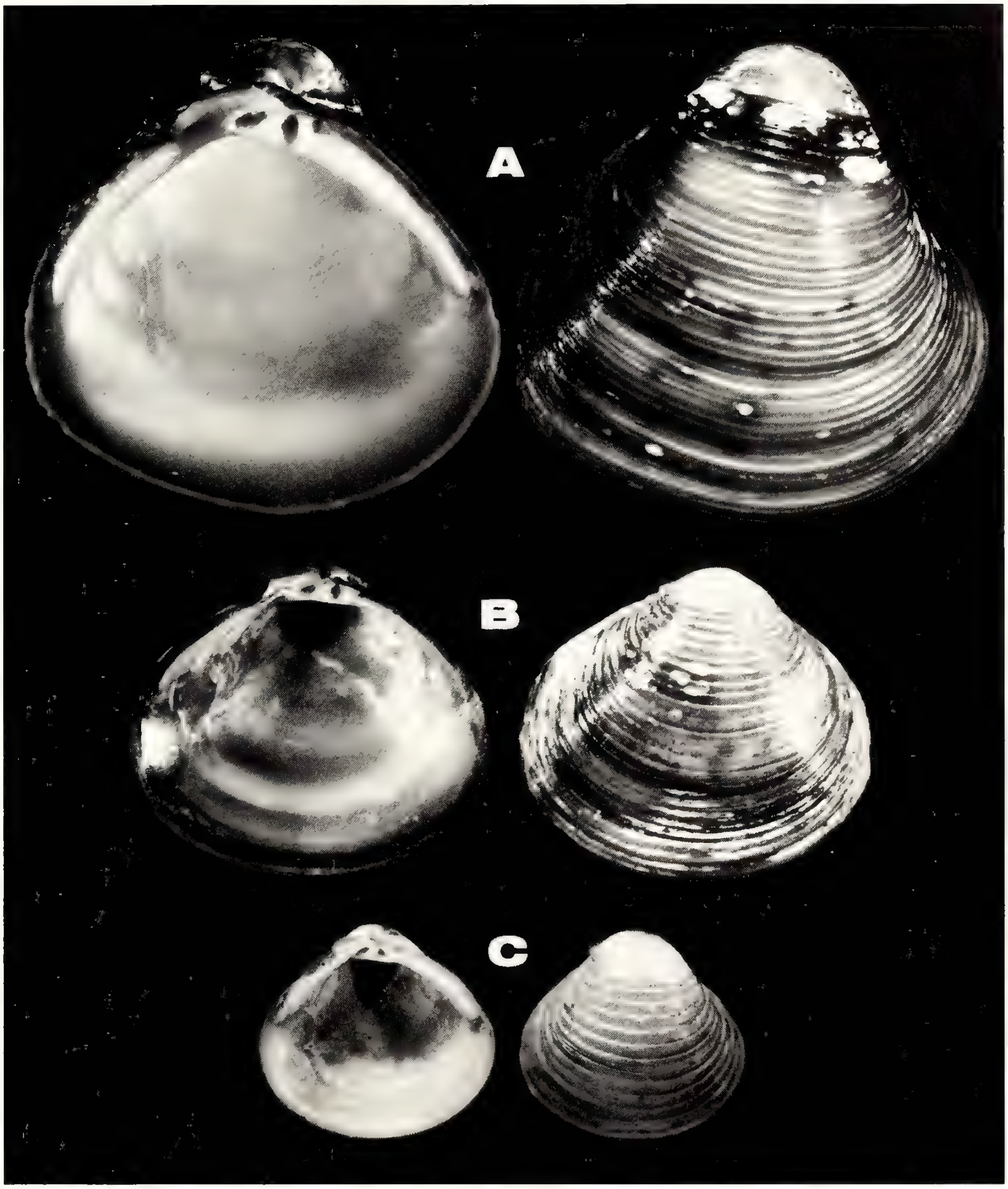

Fig. 3. A. Lectotype of *Corbicula fluminalis*; Euphrates River, Mesopotamy; U.Z.M.C. (29.9 x 30 x 21.8 mm). **B.** Neotype of *C. fluviatilis*; Canton, China; U.Z.M.C. (19.6 x 17 x 10.6 mm). **C.** Lectotype of *C. fluminea;* Canton, China; U.Z.M.C. (14.9 x 13.7 x 10.2 mm).

equilateral, integropaleate, thick and heavy. The shape is oval in juveniles and tends to be near triangular in adult specimens. The surface has well marked concentric and regular sulcations. The number of sulcations in 5 mm of shell appears to be independent of age and varies between four and eight, specimens with five or six sulcations being most frequent (Table 1, Fig. 4A). The hinge is typically heterodont with three cardinal teeth on each valve, and two crenulate lateral teeth, simple in the left valve and double in the right one. In the Miño River population the number of denticles per mm of cardinal tooth is also independent of age. It varies from five to eight, six denticles specimens being most frequent (Table, 1, Fig. 4B). The ligament is exterior and prominent (Fig. 5).

The periostracum is yellow-brown in all the specimens. The inner surface of the shell is white with a more or less violet dye (Fig. 5).

In the Miño River juveniles, it is frequent to see three strongly pigmented violet areas, one central and triangular and two lateral, just below the lateral teeth, that are also ex-

Table 1. Descriptive statistics of the Miño River population (Note: Var., variable acronym as in Fig. 2, except NºS/5mm=number of sulcations in 5 mm, and NºD/mm=number of denticles per millimeter of anterior lateral tooth; SD, standard deviation; SE, standard error; Min., minimum; Max., maximum; CV, coefficient of variation; N=45).

Var.	Mean	SD	SE	Min.	Max.	CV
L	15.82	2.66	0.39	9.7	20.0	16.81
L ⅓	14.11	2.15	0.32	8.9	16.9	15.25
L ⅔	15.26	2.63	0.39	9.3	19.5	17.21
Li	12.97	2.12	0.32	8.5	16.2	16.34
H	13.35	2.29	0.34	8.4	17.2	17.16
Hi	12.12	2.00	0.29	7.6	15.4	16.53
W	9.49	1.49	0.22	6.3	11.9	15.72
Wh	0.85	0.19	0.03	0.4	1.4	22.91
P	45.94	7.61	1.13	28.5	58.0	16.56
d	11.08	1.83	0.27	7	14.3	16.48
d'	11.23	1.83	0.27	7.1	14.3	16.27
NºS/5mm	5.44	0.96	0.14	4	8	17.75
NºD/mm	6.15	0.71	0.10	5	8	11.46
A	2.21	0.07	0.01	2.02	2.48	3.31
Add'	0.27	0.04	0.006	0.16	0.34	16.81

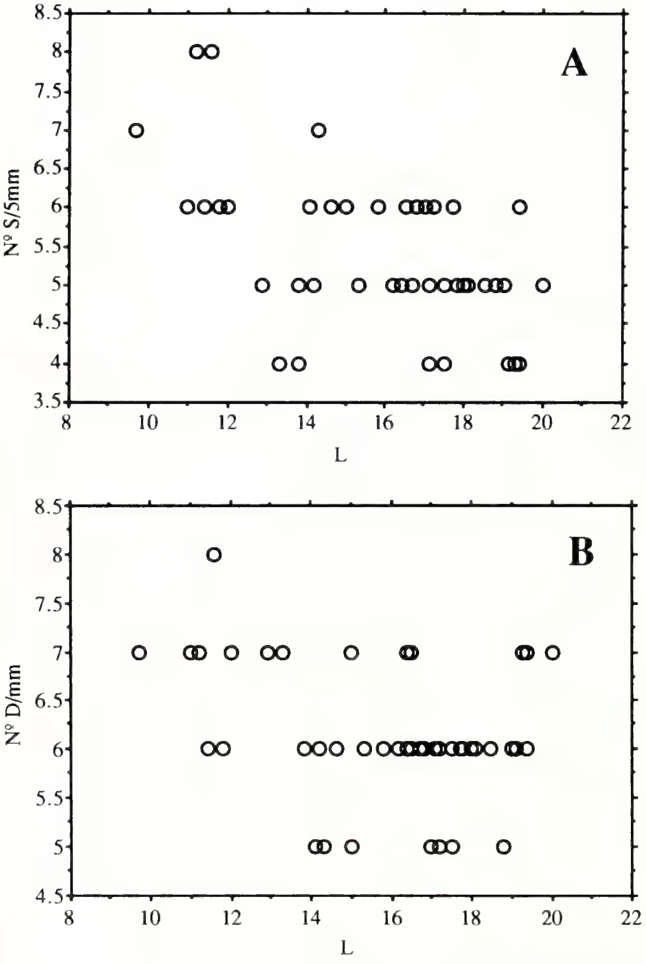

Fig. 4. *Corbicula fluminea* from the Miño River. Variation with length in the **A.** Number of sulcations per 5 mm, and **B.** Number of denticles per mm of the anterior lateral tooth.

ternally visible. The central one usually spreads and stumps in adults, with variable pigment intensity among specimens. The lateral areas surround two clear yellowish zones at both sides of the umbo, corresponding to the lunula and the scutheon which are more marked in dark specimens (Fig. 5). In the Duero River population, the violet color is more faint, the umbones are eroded and the dark lateral bands are nearly absent (Fig. 5).

In scanning micrographs of juvenile shells from the Miño River (2 - 3 mm in length) treated with sodium hypoclorite, the prodissoconch (Fig. 6A) is smooth with irregular granules in a random pattern (Fig. 6B) lacking pores and striation. Sulcations in the early dissoconch are crossed by thin radial ribs in a more or less regular disposition, thus forming a reticulate microsculpture. Downwards, the ribs disappear and they are substituted by a concentric zone with a peculiar design in which parallel and narrow sulcations are grouped forming irregular bands radially disposed (Fig. 6C). No microsculpture is observed in the later dissoconch.

Shell pores are present in both surfaces of the dissoconch being more abundant in the inner surface of the early dissoconch, where the estimated density reaches about 200 pores per square millimeter in specimens between 2 and 3 mm in length (Fig. 6D). Pores are circular in cross-section and their diameter is about 2 μm at the outer surface (Fig. 6F) and 2.5 μm at the inner one, where they are funnel-shaped (Fig. 6E, G, H, I). The pores are openings of narrow tubules that cross perpendicularly the shell (Fig. 6G), although most of them are blinded just before reaching the outer shell surface (Fig. 6H). Some of these tubules seem to be filled although the nature of the filling material is uncertain at present (Fig. 6J).

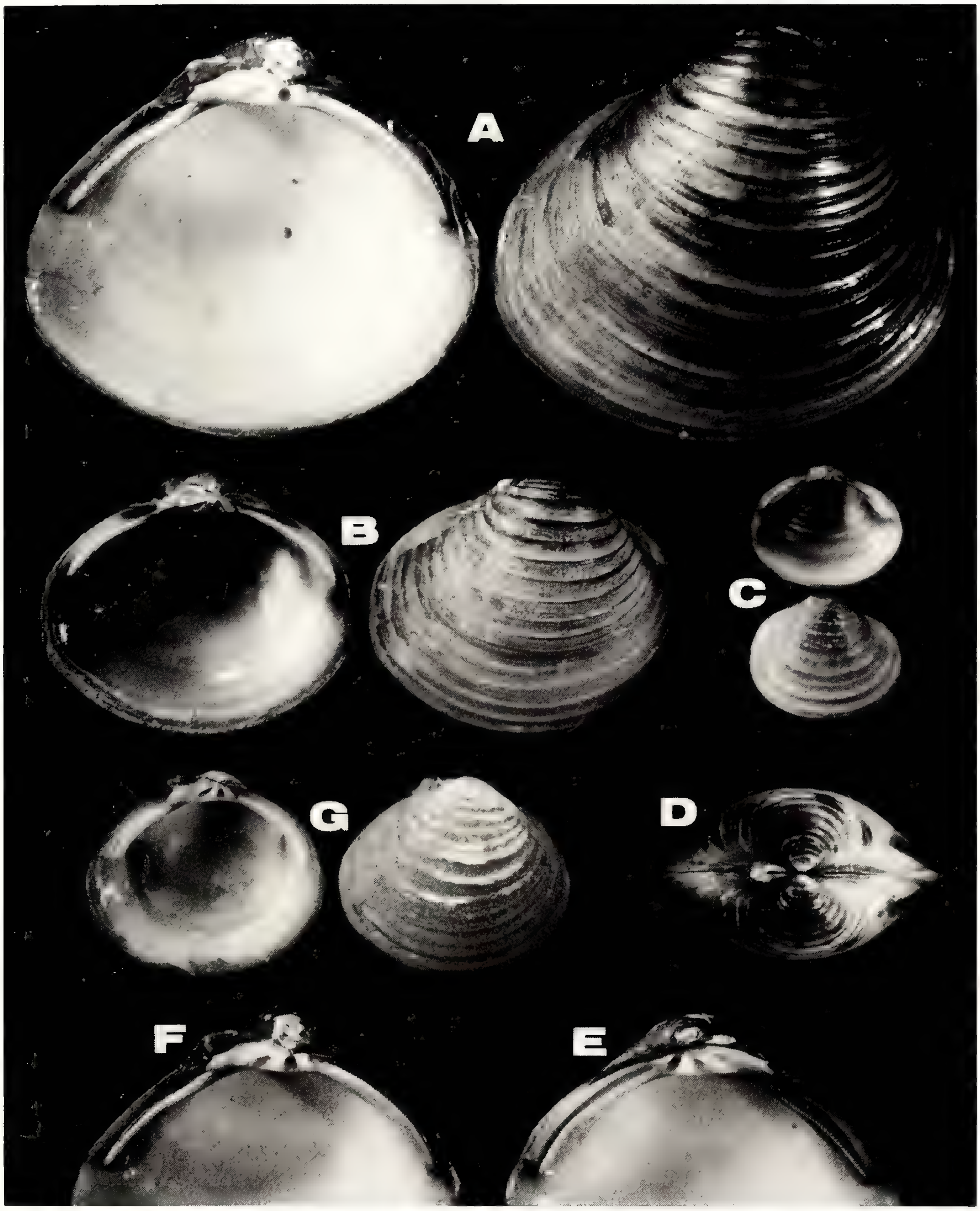

Fig. 5. *Corbicula fluminea* from Iberian Peninsula. **A, B, C.** Three different sizes from the Miño River (A=24.5 mm; B=17.2 mm; C=8 mm). **D.** Umbo of a specimen from the Miño River. **F, E.** Hinge and umbo of A. **G.** Specimen from the Douro River (13 mm).

SHELL MORPHOMETRY

Descriptive statistics for the Miño River population are given in Table 1. Variation about the means is substantial, the coefficients of variation being about 17%, except for the width of the hinge that seems to be very variable (23%), the number of teeth (11.5%) and the angle A (3.3%) which is the least variable measurement.

A similar situation is found for the raw, pooled data (Table 2). This table also shows that all variables are significantly positively correlated with L ($p < 0.0001$ except $p < 0.03$ for the A angle), suggesting that size has an important effect on shape. Most of the relationships are linear or nearly so ($r > 0.90$) and the variables roughly isometric with the standard size measure for the size range considered

Table 2. Parameters of the untransformed pooled data set for the following populations: Miño, Duero (Regua), Duero (Nagel sample), Canton (China) (Note: Var., variable acronym as in Fig. 2D; SD, standard deviation; SE, standard error; Min., minimum; Max., maximum; CV, coefficient of variation; b, slope; a, intercept; r, correlation coefficient; *, p <0.0001; **, p < 0.03; n=73).

							Regression statistics					
	Sample statistics						Variable on L			Log on Log. L		
Var.	Mean	SD	SE	Min.	Max.	CV	b	a	r	b	a	r
L ⅓	13.71	3.03	0.35	6.6	21.1	22.07	0.777	1.56	0.98*	0.918	0.04	0.99
L ⅔	15.12	3.82	0.44	7.1	27.2	25.32	0.995	-0.43	0.99*	1.025	-0.04	0.99
Li	12.84	3.19	0.37	6.0	22.5	24.86	0.827	-0.08	0.99*	1.004	-0.09	0.99
H	13.51	3.50	0.40	6.4	25.0	25.90	0.896	-0.49	0.98*	1.013	-0.08	0.98
Hi	12.36	3.15	0.36	6.0	22.7	25.50	0.802	-0.18	0.98*	0.983	-0.08	0.98
W	9.50	2.48	0.29	4.1	18.2	26.18	0.628	-0.31	0.97*	1.033	-0.25	0.97
Wh	0.96	0.36	0.04	0.4	25.0	37.16	0.076	-0.22	0.81*	1.00	-1.22	0.79
P	45.65	11.26	1.31	21.0	80.0	24.66	2.920	0.01	0.99*	1.00	0.46	0.99
d	11.19	2.84	0.33	5.4	20.7	25.42	0.730	-0.22	0.98*	0.996	-0.14	0.98
d'	11.36	2.87	0.33	5.5	21.0	25.27	0.735	-0.13	0.98*	0.990	-0.12	0.98
A	2.12	0.13	0.01	1.8	2.5	6.30	-0.008	2.26	0.25**	-0.045	0.38	0.18
Add'	0.26	0.06	0.007	0.12	0.46	24.60	0.017	0	1*	1	-1.76	1
L	15.63	3.84	0.45	7.5	27.3	24.60	——	——	——	——	——	——

(slope of log-log regression was about 1.0).

The high correlation of all variables with L indicate that a univariate approach is reasonable for size adjustment, with L as a standard size variable for it. None of these tests were significant which indicates that there are no measurements that could separate any of the four populations studied.

ANATOMY

The siphons of the Miño River *Corbicula* (Fig. 2A) are of ambarine-orange color with black spots and areas. The two siphons are internally surrounded by a black ring. Between the two siphons, and from the exhalant one, there are two well marked black lines. The siphons are surrounded by tentacles, usually with pigmented bases. Those of the inhalant siphon are longer and with black spots in the middle. There is no rule in the disposition of the fused mantle folds papillae down to the inhalant siphon. There are specimens with a single row and others with the papillae in a random pattern (Fig. 2A) and intermediate situations may be observed.

The gonadal tissue occupies, in the reproductive season, most of the visceral mass. Each gonad is formed by greenish arborescent follicles branching through the stroma of the visceral mass. The common branch leads to a single gonopore, one on each side of the body just above the excretory aperture in the latero-dorsal edge of the visceral mass (Fig. 2B).

One specimen of Goian, captured in July 1990, presented developing larvae in the inner demibranchs (Fig. 7). The larvae are bivalved and D-shaped.

DISCUSSION

All the European localities described for *Corbicula* demonstrate the species lives in substrata of sand, mud and gravel. The habitats are lotic areas receiving tidal influences with the exception of the French population cited by Girardi (1989-1990).

Physicochemical data of La Dordogne population (Mouthon, 1981) at 21°C are within the range observed in the Miño River. Conductivity values correspond in both cases to freshwaters agreeing with the habitat preferences of *Corbicula flumina* given by Morton (1982) to distinguish this species from *C. fluminalis*. The Tajo estuary population differs from the others in that the salinity varies between 4 and 18% (=7.400-30.000 μS) (Mouthon, 1981), which indicates values of salinity much higher than expected for *C. fluminea* (Morton, 1982). No data are available for the populations of the Duero River (Nagel, 1989) or the Canal du Midi (Girardi, 1989-1990).

Shell morphology of the Miño River specimens is similar to that of *Corbicula fluminea* from the UZMC collection and differs from the *C. fluminalis* lectotype (here designated) in that the last is darker, taller and more triangular than *C. fluminea*.

Shell size seems to be the most important difference among the European *Corbicula* populations. Table 3 shows maximum and minimum values of shell length for all the

Table 3. Minimum and Maximum values of shell length in European *Corbicula* populations.

Locality	Min.	Max.	Reference
Tajo Estuary	25	41	Mouthon, 1981
La Dordogne	16	20	Mouthon, 1981
Duero River	18.1	27.3	Nagel, 1989
Duero River (Regua)	7.5	13	This study
Miño River	9.7	20	This study

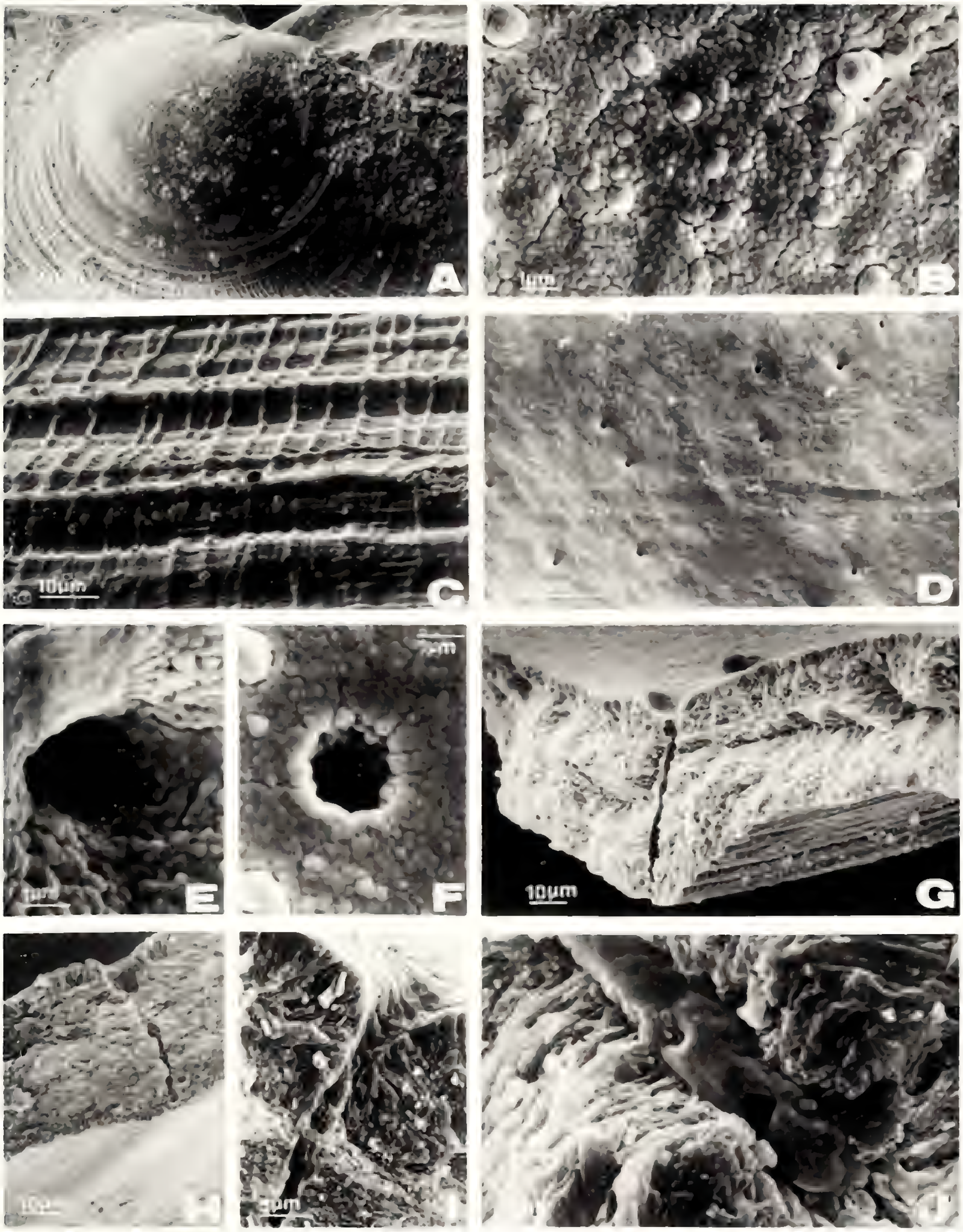

Fig. 6. *Corbicula fluminea* from Miño River. **A.** Prodissoconch. **B.** Microsculpture of the prodissoconch. **C.** Microsculpture of the early dissoconch. **D.** Pores of the inner surface. **E.** Internal pore. **F.** External pore. **G, H, I.** Sections of the shell, showing the pores and tubules. The inner surface above. **J.** Tubule filled with unknown material.

populations. The larger specimens are those of the Tajo Estuary where the smallest shells are greater than the largest ones of other three populations. However, as Britton and Morton (1979) pointed out, ''the *Corbicula* shell, in general, lacks good taxonomic markers for species discrimination'', so that according to these authors ''giving an excessive value to determinate conchological characters, it has lead up in the current taxonomic confusion''. The results suggest that size has an important effort on shape. For that reason, when shell shape of three populations (Miño River, Duero River at Regua and Duero River- Nagel coll.) and that of Canton, China, is compared after removing the effect of size on the

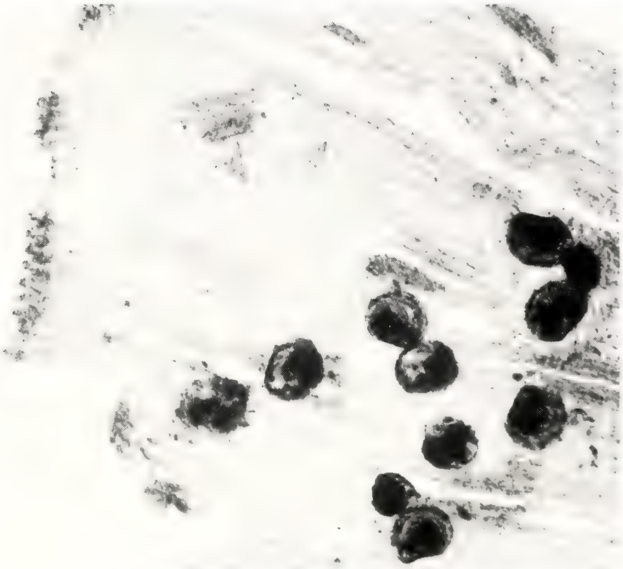

Fig. 7. Gill of Spanish *Corbicula fluminea* showing the incubated larvae (Length of the larvae = 0.2 mm).

measurements, there are no signficant differences among the european populations nor among them and the one from Canton, suggesting that all of them belong to the same species: *C. fluminea*. Unfortunately we have not enough information about the Tajo population to test whether it also belongs to the same taxonomic unit.

Mouthon (1981) cites the presence of many pores in the shell of juvenile specimens of La Dordogne. A detailed microstructural study of *Corbicula fluminea* from the Mississippi River show the existence of 196 pores per square millimeter (Tan Tiu and Prezant, 1989), which is very close to the density found in the Miño River population (200 pores per square millimeter). In scanning electron micrographs of both American and Spanish shells, it is possible to observe that pores are the openings of tubules (Fig. 6G, H), some of them filled by a material identified by the abovementioned authors as mantle extensions. We have observed similar filling structures in broken shells (Fig. 6J) but the fact that these shells were cleaned with sodium hypoclorite suggest that more studies are needed to determine the composition of the filling material and therefore the function of the tubules.

Concerning the soft parts, Britton and Morton (1979) draw the siphons and describe the differences between *Corbicula fluminea* and *C. fluminalis*. The first often has a band of pigment in the tentacles of the inhalant siphon that is absent in the last. In the exhalant siphon, *C. fluminea* shows a ring of pigment internally and is densely pigmented externally. There are more and bigger sensory tentacles around the exhalant siphon in *C. fluminalis*. The papillae of the fused mantle folds, dorsal and ventral to the siphons, form a single alternating row in *C. fluminea* and there are many more papillae arranged in a series of rows in *C. fluminalis*.

The *Corbicula* of La Dordogne has small brown spots in the base of the papillae of the two siphons and fine dark bands surrounding the mantle portion near and into the holes of the siphons (Mouthon, 1981). This pigmentation is completely absent in the Tajo River *Corbicula* (Mouthon, 1981) and is very similar to that found in the Miño specimens.

The results of this paper suggest that the number and disposition of the mantle papillae is not a useful discriminating character. The Miño River population has a very high variability including all intermediate situations (Fig. 2A). In the rest of the features they are very close to that described for *Corbicula fluminea* by Britton and Morton (1979).

Finally, Britton and Morton (1979) discriminate *Corbicula fluminea* from *C. fluminalis* by the fact that the former nourished the fertilized eggs within the inner demibranch while they are not retained in the last. Undoubtedly, this represents the most important biological difference between both species, though it is difficult to test in many samples and impossible in conchological museum collections. Figure 7 shows one specimen of the Spanish *Corbicula* population from the Miño River incubating larvae in its inner gill demibranch. This evidence, in addition to the previously discussed data of ecology, shell morphology and anatomical features, confirm the hypothesis that the Miño River population belongs to *C. fluminea*.

The available information on the other European *Corbicula* suggest that there are not enough divergences among them and *C. fluminea* populations to believe that we are dealing with a different species (except for the Tajo Estuary population). This hypothesis is also supported by the large invasive historical record of *C. fluminea* (McMahon, 1982, 1983 and references), not shared by any other *Corbicula* species and the wide ecological range both in natural habitats as in colonized ones.

Regarding ecological effects on the native fauna, the disappearance of *Pisidium amnicum* at Goian was coincident with the *Microcystis aeruginosa* bloom and also with the demographic increase of *Corbicula fluminea*. For this reason it is impossible to assess if only one of these phenomena or both were responsible for this extinction.

Further research about population dynamics and reproductive strategy must be conducted in order to elucidate the growth and invasive speed of *Corbicula fluminea* in Europe, but it is a fact that we are witnessing an introduction of this invasive bivalve in the continent.

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Genetic relationships among Asian *Corbicula:* Thai clams are referable to topotypic Chinese *Corbicula fluminea*

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Abstract. A survey of 28 electrophoretically detected allozyme loci revealed that Thai *Corbicula* are weakly differentiated (Nei's unbiased genetic distance, $D = 0.12\text{-}0.16$) from *Corbicula fluminea* from the type locality in southern China, 1800 km away. This finding supports our earlier proposal that 20 nominal *Corbicula* species from Thailand are junior synonyms of the widespread and conchologically variable *C. fluminea.*

We have shown recently that 21 nominal species of freshwater clams, *Corbicula*, from Thailand are genetically indistinguishable and most probably referable to the widespread Asian species *C. fluminea* (Müller, 1774) (Kijviriya *et al.*, 1991). We found little variation at 24 allozyme loci in *Corbicula* collected from 40 sites up to 1500 km apart in Thailand. Thirty-five of the samples were found to be genetically identical; clustering at insignificant ($D < 0.01$) multilocus genetic distances (Nei, 1978). The remaining five samples (from northeast Thailand) were weakly differentiated from the others with $D < 0.04$. The low levels of genetic differentiation led us to suggest that 20 Thai species were junior synonyms of the earliest named local taxon, *C. fluminea*, a population of which was recognised from the Chao Phraya River, Bangkok, by Brandt (1974). We argued that our proposed revision would be supported by the demonstration that the Thai *Corbicula* are genetically similar to Chinese clams from the type locality of *C. fluminea.* We now present a genetic comparison of the Thai clams with topotypic *C. fluminea* from south China and show that the proposed synonymy was appropriate.

MATERIALS AND METHODS

To test the hypothesis that the Thai clams are genetically similar to topotypic *Corbicula fluminea* we performed a multilocus comparison of two samples of *Corbicula* from northeast Thailand and one from Hong Kong, 1800 km to the northeast. One of the Thai samples had been shown previously to be genetically identical to putative *C. fluminea* from Thailand but its relationship to topotypic clams was unknown. The three samples were:

Thai 1. Collected from Ubonrat Reservoir, Khon Kaen Province, northeast Thailand. Voucher specimens in Museum, Center for Applied Malacology and Entomology, Faculty of Science, Mahidol University (MUFS-THOO-167) and Los Angeles County Museum of Natural History (LACM 85-366.1). These clams were identified originally using Brandt's (1974) criteria as *Corbicula lydigiana* Prime, 1861, by Kijviriya (1990), and subsequently referred to as Sample 23 in Kijviriya *et al.* (1991), where they were shown to be genetically identical to putative *C. fluminea* from the Chao Phraya River, Bangkok.

Thai 2. Collected at Ban Huikom, Phibun Mangsahan District, Ubon Ratchathani Province, northeast Thailand. Conchologically very similar to Thai 1; specific identity not determined. Voucher specimens: MUFS-THOO-192 and LACM 85-367.1.

China. Collected at Ping Long Village, Lam Tseun River Valley, New Territories, Hong Kong. Shell color and morphometric variation in this population has been described in detail by Morton (1987). Voucher specimens: LACM 85-368.1.

Clams were frozen at -70°C immediately after collection and handcarried to the senior author's laboratory for genetic analysis. Starch gel electrophoretic separation of allozymes extracted from whole body homogenates was according to the methods of Kijviriya *et al.* (1991). For 20 loci the specific methods are given by Kijviriya *et al.* (1991: see Table 1 for full names and Enzyme Commission numbers): *Aat-1, Aat-2, Es-1, Es-4, Es-5, G6pdh, Gpi, Idh-1, Idh-2, Mdh-1, Mdh-2, Mdhp-1, Mdhp-2, Pep-A-1, Pep-B-2, Pep-B-3, Pgdh, Pgm-1, Pgm-2, Xdh.* Three additional loci [*Acp* (E.C. 3.1.3.2), *Cat* (1.11.1.6), *Ldh* (1.1.1.27)] were resolved on the TC 6.0 buffer described therein, and five others were resolved

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on the TC 6.8 buffer used by Staub *et al.* (1990); *Gapdh* (1.2.1.12), *G3pdh* (1.1.1.8), *Mpi* (5.3.1.8), *Sod-1, Sod-2* (1.15.1.1). Data consisting of genotypes for individual clams scored at all 28 loci were analyzed and Nei's genetic identities *(I)* and unbiased genetic distances *(D)* (Nei, 1972, 1978, respectively) were calculated using the BIOSYS-1 computer programs (Swofford and Selander, 1981).

RESULTS

Allozymic variation is summarized in Table 1. Twenty-one of the 28 loci showed no detectable variation; seven loci varied geographically. Both Thai samples were isogenic. The Chinese sample showed low levels of genetic variabiltiy, with diallelic systems at four loci and genotypes in panmictic frequencies. The Chinese clams are slightly more variable than the most variable samples reported previously from Thailand (Kijviriya *et al.*, 1991) due to the addition of another polymorphic locus, *Mpi*, to the survey.

The Thai 1 sample is genetically identical to Sample 23 of Kijviriya *et al.* (1991), which was collected at the same reservoir. Thai 2 was found to be very similar to Sample 20 of Kijviriya *et al.* (1991), which was collected from the same district. The small genetic distance (Table 2: $D = 0.04$) between Thai 1 and Thai 2 is similar to that reported between Samples 20 and 23 and typical of the maximum genetic differentiation detected previously among Thai *Corbicula*. The fixed difference at *Es-5* had been detected previously in Thai clams.

The Thai *Corbicula* are very similar to topotypic *C. fluminea* from Hong Kong. The mean genetic distance, $D = 0.14$, is largely due to fixed differences at *Mdh-1, Mpi,* and *Pgm-1.*

Table 1. Genetic variability in Asian *Corbicula**.

Sample:	Thai 1	Thai 2	China
Locus		Allele frequency	
Aat-2^{a}	1.00	1.00	0.61
Es-5^{a}	1.00	0.00	0.00
Gpi^{b}	1.00	1.00	0.75
Mdh-1^{a}	1.00	1.00	0.00
Mpi^{b}	1.00	1.00	0.5/0.5
Pep-A-1^{a}	1.00	1.00	0.64
Pgm-1^{a}	1.00	1.00	0.00
Summary statistics			
N	16	17.5	17.7
A	1.0	1.0	1.1
P	0.00	0.00	0.14
H	0.00	0.00	0.07

*Summary statistics are: *N*, mean sample size; *A*, mean no. of alleles per locus; *P*, proportion of loci polymorphic; *H*, mean individual heterozygosity. Each variable locus has two alleles except for triallelic *Mpi*, where alleles *a* and *c* co-occur in the Chinese sample.

Table 2. Matrix of genetic distance values.

Sample	Thai 1	Thai 2
Thai 1	---	
Thai 2	0.04	---
China	0.16	0.12

DISCUSSION

The genetic identity among the Asian clams studied here is slightly higher than that reported in an earlier 12-locus comparison of samples from Hong Kong and the United States (Smith *et al.*, 1979): $I = 0.87$ vs. 0.84. The Thai *Corbicula fluminea* are thus more similar to those of China than the latter are to their trans-Pacific derivatives.

Although there is no simple relationship between genetic distance and taxonomic level the $D = 0.14$ value reported here is within the range found among conspecific populations of geographically widespread molluscs and other animals (Davis, 1983; Thorpe, 1983; Woodruff *et al.*, 1988). Cases of interspecific comparisons with $D < 0.14$ are known but, in such cases, species status rests on other criteria (especially behavioral traits that could function as reproductive isolating mechanisms or species recognition cues, postmating sterility barriers, chromosomal reorganization, etc.) and genetic similarity merely reflects the recency of cladogenesis. We know of no such criteria which might affect our interpretation of the genetic similarities discovered among Asian *Corbicula*. Detailed studies of anatomical variation in clams from China (Morton, 1987) and Thailand (Kijviriya, 1990) failed to reveal any taxonomically significant variation. Only in the case of conchological features (shell size, shape, sculpture and color), has significant local and geographic variation been documented. Such conspicuous conchological variation, employed by Brandt (1974) to recognize 28 *Corbicula* species in Thailand, is now seen to be taxonomically irrelevant. Morton's (1986) opinion, that most or all of Brandt's taxa are junior synonyms of *C. fluminea*, is supported. We reaffirm our recommendation (Kijviriya *et al.*, 1991) that 20 nominal Thai taxa for which we have genetic data be synonymized with *C. fluminea* (Müller, 1774).

Finally, our finding of only moderate differentiation within geographically widespread populations of *Corbicula fluminea* on the Asian mainland contrasts with the higher levels of differentiation ($I = 0.3$) reported between Japanese and Philippine clams by Smith *et al.* (1979). A comprehensive allozymic survey in Asia is now required to establish whether the island populations merit specific recognition. Such a survey could also resolve two issues involving the North American *C. fluminea*: the identification of the source population(s) and the number of successful colonizations. Although available genetic data support an Asian mainland origin hypothesis, they do not preclude an island origin, or multiple introductions from either source. Given the apparent genetic uniformity of the Asian mainland populations, it could be difficult, however, to reconstruct the events surrounding their introduction to North America using allozymes.

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Genetic structure and heterozygosity-related fitness effects in the marine snail *Littorina littorea*

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Abstract. The relationships among rate of oxygen consumption under routine and starved conditions, soft tissue dry weight, shell growth rate and heterozygosity at polymorphic allozyme loci were investigated in 86 individuals of the common periwinkle, *Littorina littorea* (Linnaeus, 1758). Oxygen consumption was measured at the time of collection and after 14 days starvation using a micro-Winkler method. Soft tissue dry weight was estimated from shell height using a regression equation developed from analysis of a set of 34 additional snails. Shell growth rate was estimated as distance between successive lines in thin sections through the growing edge of the shell. Heterozygosity was studied using conventional starch gel electrophoretic techniques to examine enzyme systems controlled by 34 loci; 11 of the loci were polymorphic. The mean observed heterozygosity per locus per individual was 0.073. Continuous variables were adjusted for differences in estimated dry weight by using linear regression to convert all measurements to a standard dry weight. Only for growth rate was there a significant positive association with dry weight. The weight-adjusted values were then tested for an effect of heterozygosity using linear regression. There was no evidence for an association between level of heterozygosity and oxygen consumption under either routine or starved conditions. However, starvation caused a significant depression in oxygen consumption, in paired comparisons. There was no detectable association between heterozygosity and shell growth rate.

Genetic studies of marine mollusc populations have reported several unexpected findings, including deficiencies in the numbers of heterozygous individuals and correlations between estimates of an individual's overall level of heterozygosity and various surrogate measures of fitness such as growth or viability (Mitton and Grant, 1984; Zouros and Foltz, 1984, 1987). Among marine molluscs, there is abundant evidence for age- or size-dependent changes in allele frequencies and in the level of observed heterozygosity for numerous allozyme loci. One common pattern is for the heterozygosity to increase (or the deficiency of heterozygotes to decrease) among older or larger animals, suggesting an apparent viability advantage of more heterozygous individuals. There is also an extensive literature reporting positive correlations between allozyme heterozygosity and growth rate in marine molluscs and other organisms; several conclusions have emerged from this work. First, the apparent correlation between heterozygosity and growth rate can be related at the physiological level to either a lower cost of routine metabolism (Koehn and Shumway, 1982; Garton, 1984), a higher feeding rate (Garton, 1984; Holley and Foltz, 1987), or both, in highly heterozygous individuals. Hawkins *et al.* (1986, 1989) have attempted to integrate these findings with more traditional concepts in molluscan physiology. They argue that the greater metabolic efficiency of more heterozygous individuals results from lower rates of protein turnover in such individuals, not from lower rates of energy metabolism. Further, they suggest that low intensities of protein turnover reduce the energy required for maintenance, with some of the energy saved being used to support increased feeding rates. A second approach has been to compare heterozygosity-fitness correlations from various studies and organisms in a search for general trends. For example, Zouros (1987) reported that significant positive correlations between heterozygosity and fitness components were more likely to be found in marine molluscs if (1) the allozyme loci showed deficiencies in the numbers of heterozygous individuals (compared to Hardy-Weinberg expectations), and (2) the sample came from a natural population rather than laboratory populations derived from a small number of parents. These two findings suggest an influence of population genetic structure on the occurrence of heterozygosity-fitness correlations. The association between degree of heterzygote deficiency and occurrence of heterozygosity-fitness correlations has not been satisfactorily explained, and seems counter-intuitive. Although several different hypotheses have been proposed to explain this association (see below), present data are insufficient to decide among them. More data are needed, particularly to determine if the association between heterozygote deficiency and heterozygosity/fitness correlations is of wide occurrence. The present study examines genetic structure, heterozygosity, weight, growth rate and oxygen consumption rate in a natural population sample of the marine snail *Littorina littorea* (Linnaeus, 1758).

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*Deceased 18 January 1990

MATERIALS AND METHODS

A total of 86 *Littorina littorea* (shell height range 16.6—26.2 mm) was collected near West Boothbay Harbor, Maine (during the same tidal cycle and from the same shore height) in the spring of 1987. Immediately after collection, each snail was marked individually with a small plastic tag and its (routine) oxygen consumption rate determined. The snails were then held in tanks supplied with running seawater without food for 14 days, after which rates of oxygen consumption were again measured. Seawater temperatures ranged from 8-12°C during the experiments, and all measurements of oxygen consumption were made under ambient conditions. Oxygen consumption rates were measured on individual animals in 70 ml experimental chambers using a micro-Winkler technique (Burke, 1962). The snails were allowed to equilibrate for 1 hr, during which time the water was aerated. Measurements were carried out over a period of approximately 3 hrs; total oxygen concentration in the experimental chambers never fell below 70% saturation. Controls were run using identical vessels with no animals. The snails were then placed in large (2.0 m x 0.5 m x 0.5 m) cages at mid-tide level for four weeks. Ample supplies of *Ulva* and *Enteromorpha* were maintained in the cages as a food source. The snails were removed from the cage and the shell height of each animal was measured. The free growing edge of each shell was removed with a diamond saw, and the soft tissues were removed and frozen at -80°C for later allozyme analysis.

Shells were preserved in 70% alcohol containing a small quantity of borax and air-shipped to Menai Bridge, Wales, for growth measurements in the laboratory of D. J. Crisp. The most recently deposited 2 or 3 mm at the lip of each shell were embedded in resin. Sections were cut parallel to the direction of growth, and the cut surface ground on wet and dry paper and polished on a cloth soaked in "Brasso." The polished surface was etched in 0.01 M HCl for 10-20 min, and acetate peel replicas of the dry surface prepared using the technique described by Ekaratne and Crisp (1982). The peels were examined microscopically and the shell growth rate for each animal estimated from the width of the most recently deposited band. The growth bands were reasonably assumed to correspond to the most recent tidal cycle, because similar bands have been shown to be tidally-produced in *Littorina littorea* from Menai Strait, Wales (Ekaratne and Crisp, 1982, 1984). Soft tissue dry weight of each animal was estimated by a regression equation obtained from a set of 34 additional snails collected near West Boothbay Harbor. This set had a mean shell height of 18.6 mm (range 6.5—28.2 mm) and a mean soft tissue dry weight of 0.146 g (range 0.002—0.384 g). The regression equation relating soft tissue dry weight (Y) and shell height (X) was $\log_e(Y) = -12.44 + 3.49 \cdot \log_e(X)$, $P < 0.0001$, $R^2 = 0.98$. The mean estimated soft tissue dry weight of the 86 snails was 0.153 g (range 0.074—0.314 g).

The frozen tissue samples were air-shipped to the laboratory of D. W. Foltz, where they were processed and analyzed electrophoretically by standard methods (e.g. Harris and Hopkinson, 1976). In all, 34 enzyme loci were resolved. Alleles at each polymorphic locus were designated by numbers indicating mobility relative to the most common allele at that locus, which was designated "100"; negative numbers indicated cathodally migrating bands. For enzymes with multiple isozymic forms, loci were numbered sequentially starting with the most anodally-migrating system. Allele frequencies, fixation indices (F) and observed and expected heterozygosities for each locus were calculated using standard formulas (e.g. Hedrick, 1983). All data were analyzed by the Statistical Analysis System (SAS Institute, Inc., 1985).

RESULTS

Of the 34 enzyme loci examined, 11 were polymorphic (see Table 1 for allele frequencies and single-locus observed heterozygosities). The fixation index (F) for each polymorphic locus was close to 0, indicating no significant departures from Hardy-Weinberg equilibrium. The average F was 0.003 (range -0.051—0.131). The average number of heterozygous loci per individual was 2.49 (range 0—5). The frequency of each heterozygosity class was plotted and compared with the expected frequency derived from the 11 single-locus expected heterozygosities (Fig. 1). The distribution of observed heterozygosity was more platykurtic than the expected distribution, with an excess of both low-heterozygosity and high-heterozygosity individuals.

Continuous variables (growth rate, routine and starved oxygen consumption rate) were $\log_e$-transformed prior to analysis (to help ensure that each dependent variable had a normal distribution and uniform variance) and were adjusted for differences in estimated soft tissue dry weight by using linear regression to convert all measurements to a standard dry weight (0.146 grams). As expected, there was a significant positive effect of dry weight on growth rate ($P < 0.03$), but no detectable effect of dry weight on routine ($P > 0.07$) or starved ($P > 0.26$) VO_2. The finding of no association between oxygen consumption under routine or starved conditions and estimated soft tissue dry weight was unexpected. It differs from previous studies of *Littorina littorea* (e.g. Newell and Roy, 1973) that have found a positive correlation between oxygen consumption and dry tissue weight. The lack of a correlation is most likely due to the absence of extremely low-weight individuals in the present sample. For example, in Newell and Roy's (1973) study the range for estimated soft tissue dry weight was 2—160 mg, whereas the corresponding range in the present study was 70—300 mg. There was a significant depression in oxygen consumption after starvation for 14 days. Previous studies of the effect of starvation on oxygen consumption in pulmonate and prosobranch molluscs (summarized by Studier and Pace, 1978) have variously found that oxygen consumption rates increase, decrease or remain constant in starved animals. Factors responsible for such different responses could include length of starvation period, acclimation temperature or sex differences. Fig. 2 presents growth rate (μm/tidal cycle), adjusted for dry weight differences, and dry weight (in grams) for different levels of heterozygosity. Multiple-locus heterozygosity was not a significant source of variation for either adjusted growth rate ($P > 0.07$, $R^2 = 0.04$) or dry weight ($P < 0.77$), $R^2 < 0.01$). Single-locus heterozygosity for each of the 11 polymorphic loci also was not a significant source of variation for either adjusted growth rate or dry weight, after allowing for multiple tests (results not shown). Fig. 3 presents Vo_2

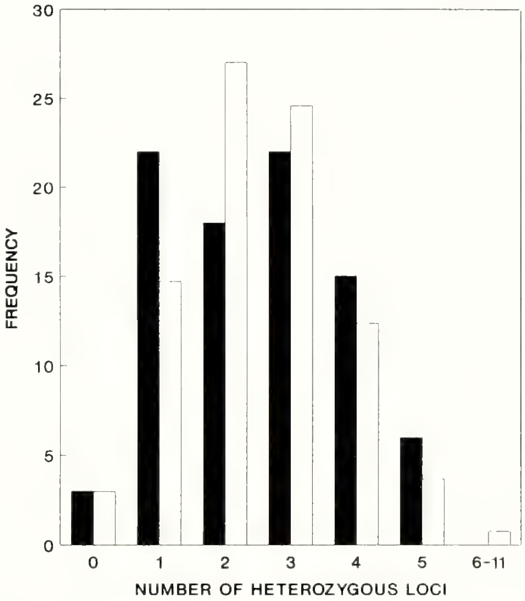

Fig. 1. Observed (filled bars) and expected (open bars) numbers of individuals with various numbers of heterozygous loci (out of 34 examined loci) in *Littorina littorea*.

Table 1. Enzyme commission (E.C.) numbers, allele frequencies and observed heterozygosities (H_0), ± 1 standard error, at 11 polymorphic allozyme loci in *Littorina littorea*.

Locus	E.C. No.	Allele	Frequency	Locus	E.C. No.	Allele	Frequency
Acon-1	4.2.1.3	107	.023 ± .011	*Pep*	3.4.-.-	112	.017 ± .010
		100	.971 ± .013			100	.983 ± .010
		95	.006 ± .006			H_0	.035 ± .020
		H_0	.058 ± .025				
Acon-2	4.2.1.3	208	.006 ± .006	*6-Pgd*	1.1.1.44	175	.029 ± .013
		146	.122 ± .025			147	.238 ± .032
		100	.872 ± .025			133	.047 ± .016
		H_0	.232 ± .046			100	.686 ± .035
						H_0	.488 ± .054
Ck	2.7.3.2	127	.052 ± .017	*Pgi*	5.3.1.9	107	.047 ± .016
		119	.012 ± .008			100	.936 ± .019
		100	.936 ± .019			93	.011 ± .008
		H_0	.128 ± .036			85	.006 ± .006
						H_0	.128 ± .036
Est-1	3.1.1.1	105	.011 ± .008	*Pgm-1*	5.4.2.2	100	.913 ± .022
		100	.989 ± .008			71	.087 ± .022
		H_0	.023 ± .016			H_0	.151 ± .038
Est-3	3.1.1.1	-119	.273 ± .034	*Pgm-2*	5.4.2.2	126	.047 ± .016
		-100	.401 ± .038			111	.106 ± .023
		-67	.303 ± .035			100	.694 ± .035
		-59	.023 ± .011			83	.153 ± .028
		H_0	.698 ± .050			H_0	.447 ± .054
Glydh	1.1.1.29	116	.064 ± .019				
		100	.936 ± .019	Average*		H_0	.073 ± .005
		H_0	.105 ± .033				

*Average H_0 includes the following 23 monomorphic loci: *Ada* (3.4.4.4); *Adh* (1.5.1.17); *Ald* (4.1.2.13); *Alkp* (3.1.3.1); *Ark* (2.7.3.3); *Est-2* (3.1.1.1); *Fum* (4.2.1.2); *Got* (2.6.1.1); *G-6-Pdh* (1.1.1.49); *Gpt* (2.6.1.2); *Gpdh* (1.1.1.8); *Idh-1* (1.1.1.42); *Idh-2* (1.1.1.42); *Ipo* (1.15.1.1); *Lap* (3.4.-.-); *Mdh* (1.1.1.37); *Me* (1.1.1.40); *Mpi* (5.3.1.8); *Nsp* (2.4.2.1); *Odh* (1.5.1.11); *Pep (LGG)* (3.4.-.-); *Sdh* (1.1.1.14); *Xdh* (1.1.1.204).

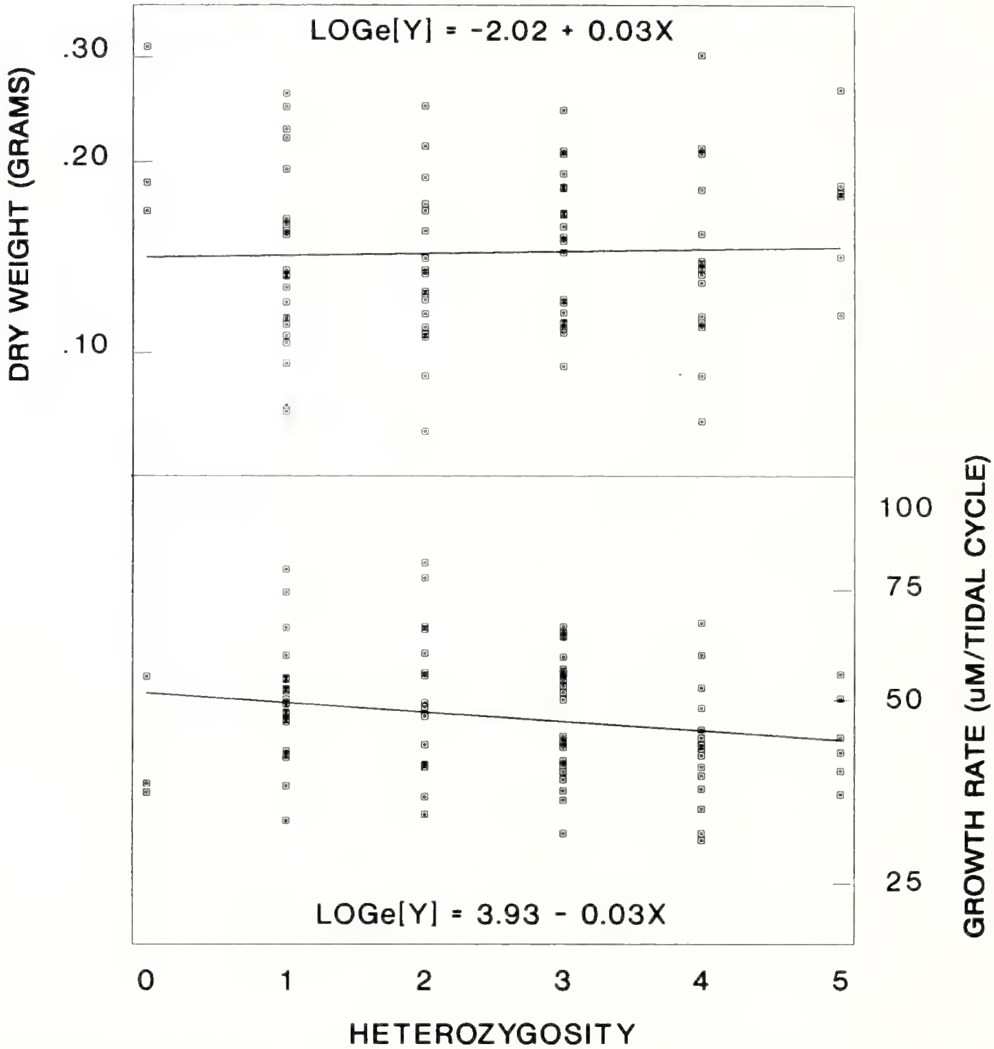

Fig. 2. Semi-logarithmic plots of estimated soft tissue dry weight (upper panel) and growth rate (lower panel) verus heterozygosity in *Littorina littorea*. Regression lines and equations are also shown, but are not statistically significant.

(ml $O_2 \cdot hr^{-1}$) under routine and starved conditions for different levels of heterozygosity. The effect of heterozygosity on adjusted oxygen consumption rate was not significant when tested by linear regression, under either routine ($P > 0.65$) or starved ($P > 0.85$) conditions. There was a significant reduction ($P < 0.0001$ by paired t-test) in adjusted oxygen consumption rate under starved conditions (mean = 0.092 ml $O_2 \cdot hr^{-1}$) when compared to the corresponding mean value (0.113) under initial conditions.

DISCUSSION

The observed heterozygosity in this study (0.073 ± 0.005) is slightly higher than that reported (0.04) in previous studies of *Littorina littorea* (Fevolden and Garner, 1987; Janson, 1987). Fevolden and Garner (1987) found no evidence for heterozygote excesses or deficiencies. They also looked for genetic differences between fast-growing and slow-growing snails at the *6-Pgd* locus, with negative results. The present study extends that conclusion to a larger set of heterozygous loci and to oxygen consumption rate comparisons. Plots of VO_2 versus heterozygosity for both routine and starved conditions gave no suggestion of an association for either treatment, although the three snails with 0 observed heterozygosity had very low oxygen consumption rates. As seen in Fig. 2, these animals also had very high weights. Although the oxygen consumption rates were adjusted for the (linear) effect of $\log_e$-transformed dry weight, there could have been some residual effect of weight differences on oxygen consumption.

The previous literature on allozyme heterozygosity-fitness correlations has been summarized by Mitton and Grant (1984), Zouros and Foltz (1987) and Zouros (1987). As noted

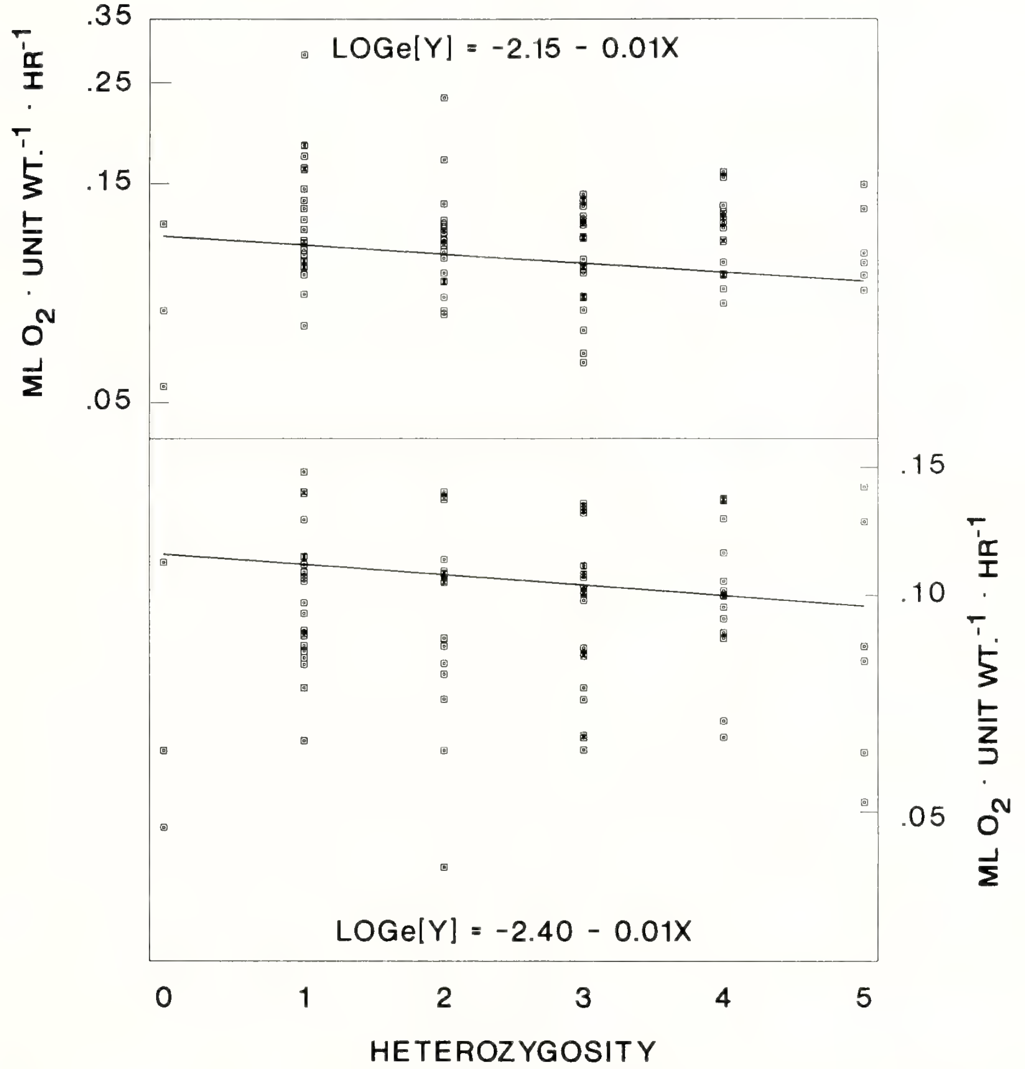

Fig. 3. Semi-logarithmic plots of oxygen consumption rate under fed conditions (upper panel) and under 14-day starvation conditions (lower panel) versus heterozygosity in *Littorina littorea*. Regression lines and equations are also shown, but are not statistically significant.

above, heterozygosity-fitness correlations are more likely to be found when the same set of allozyme loci exhibits a deficiency in the number of heterozygous individuals than when they do not. The data obtained for *Littorina littorea* in this study and by Fevolden and Garner (1987) are consistent with the suggestion that heterozygosity-fitness correlations in natural populations of marine molluscs are largely absent when genotype frequencies closely approximate the Hardy-Weinberg expectations. Two previous studies of heterozygosity and growth rate in marine gastropods (Fujino, 1978; Garton, 1984) reported the co-occurrence of heterozygote deficiencies and heterozygosity-size (or heterozygosity-growth rate) correlations. Despite the seeming contradiction between deficiencies in the numbers of heterozygotes (compared to Hardy-Weinberg expectations) and apparent heterozygote superiority at the same loci, positive associations between these two phenomena have been found in numerous studies. This pattern occurs when different species are compared (Zouros, 1987; Zouros and Mallet, 1989) and also when different loci within a single species are compared (Gaffney *et al.*, 1990). As reviewed by Zouros *et al.* (1988) and Gaffney *et al.* (1990), at least three explanations can potentially explain the co-occurrence of heterozygote deficiencies and heterozygosity-fitness correlations at the same set of loci. First, molecular imprinting could account for both phenomena (Chakraborty, 1989). Second, a high rate of chromosomal mutation (Thiriot-Quievreux, 1986; Thiriot-Quievreux *et al.*, 1988) and/or a high rate of single-gene mutation, could be responsible for apparent heterozygote deficiencies through production of null mutations, where nulls could either be point mutations resulting in loss of activity at a single allozyme locus or else multi-locus deletions with presumably larger fitness effects. A high mutation rate could also cause apparent heterozygosity-fitness correlations, either through direct reduction in fitness of allozyme active/null heterozygous genotypes (Zouros and Foltz, 1987) or through associative overdominance (Zouros, 1987). Third, partial inbreeding will generate both a deficiency of heterozygotes at individual loci and an inter-locus correlation in the degree of heterozygosity (Haldane, 1949; Bennett and Binet, 1956). These inter-locus correlations can generate apparent heterozygote superiority through inbreeding depression (Strauss, 1986; Bush *et al.*, 1987) even in the absence of any direct fitness effect of the loci examined. As yet, there is insufficient knowledge about the genetics and population structure of marine molluscs to allow these possibilities to be tested.

ACKNOWLEDGMENTS

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The arm crown in cephalopod development and evolution: a discussion of morphological and behavioral homologies

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Abstract. Capture and manipulation of prey is the primary function of the arms in cephalopods, but they also take on various other prehensile functions as well as propulsive ones (e.g. 'walking' in octopus). In many instances they act as visual signal effectors as well. The entire arm crown can be involved in concerted actions, or individual pairs of arms (or an individual arm in the case of certain hectocotyli) can act in a discrete manner.

This paper discusses the problem of arm identity and homology in order to provide a basis for the comparison of arm action patterns and arm postures in different cephalopod groups. Emphasis is placed on data derived from the morphogenetic pathway that leads from a uniform embryonic anlage, through subdivision into distinct arm rudiments, to the differentiation of arms. These data support the homology between the arm crowns of decapods and octopods. Furthermore, there is good evidence for the homology of arm pairs at three positions: dorsal arms, ventral arms, ventrolateral arms (=tentacles of decapods).

The study of animal behavior is related closely to the fields of animal physiology and functional morphology. Bullock (1965: 454) stated: ''Behavior is carried out by effectors''; they have physiological characteristics that are affected by their morphological properties, the latter of course include the arrangement of the nerves controlling and coordinating the actions of effectors. These intrinsic processes and their underlying mechanisms are studied by neurobiologists who may also be interested in the coadaptation of receptor and effector systems. Behavioral ecologists, on the other hand, investigate the extrinsic effects of behavior to assess specific behavioral adaptations to an environment. The evolutionary perspective of the whole problem is emphasized by the term adaptation. Here the function of behavior is viewed against the historical background of organismal change through time.

From the comparative study of functional morphology one can conclude that structural modifications have occurred only within rather narrow limits in the phylogenetic history of organisms in general (Riedl, 1978). The question of whether the same is true for behavior was raised by ethologists early in this century, and from the comparative study of behavior in more or less closely related species they concluded that certain behavioral features can indeed be considered as discrete heritable characters of the phenotype that must somehow be programmed in the genome, much like morphological characters [see Lorenz (1978) for a review].

If behavior is thus studied in a conceptual framework of evolutionary structure, the basic problem to be approached is the homology of behavior characters. The crucial question is whether homology of behavior characters can be established only relative to homologous effector systems, or whether homologies exist at higher levels of neural integration.

The arms of cephalopods provide an interesting example of co-ordinated effector systems built into a higher integration structure, the arm crown and brachial lobe system, with more or less clearly recognizable homologies at the lower structural levels. This paper discusses arm identities in coleoid cephalopods, dealing in particular with the significance of homology recognition at different levels of integration. The roles played by the arms in one or several superimposed functional contexts (e.g. feeding, burying, signalling) are thus considered from the viewpoint of 'multi purpose' effector systems in a way that is intermediate between the approaches of neurobiologists and behavioral ecologists.

THE HOMOLOGY CONCEPT AND ITS APPLICABILITY

Homology is a basic concept underlying all comparative studies in biology [see Roth (1991) for a review]. Homologies can be defined in different ways, either excluding or including the criterion of resemblance in the definition. Dohle (1989: 383) makes a clear distinction between homology and transformation, homology representing ''conformity based on identical instruction for differentiation, handed on by identical replication'', whereas transformation represents the ''gradual modification of an initial structure leading to extensive dissimilarity that may even end in an unrecognizable condition''; he therefore considers resemblance an essential ingredient of homology.

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In all instances, the 'practical' aim of the search for homology is sorting out non-homologous features, which are characterized by resemblance that is *not* "caused by continuity of information" (Van Valen, 1982: 305). As phylogenetic relationships between different organisms can only be recognized on the basis of truly homologous features, i.e. "those that stem phylogenetically from the same feature (or condition) in the immediate common ancestor of these organisms" (Bock, 1989: 331), one is faced with the danger of circularity; it can only be circumvented by the application of very strict rules in testing the homology hypothesis.

As structures that can be subjected to a homology test are generally defined on the basis of recognizable component elements, which can represent 'standard parts' at lower integration levels (Riedl, 1978), one ultimately deals with increasingly generalized standard parts ending at the cellular and molecular levels. In order to resolve this problem of 'infinite regression', complex patterns of corresponding substructures are required for homology propositions (Dohle, 1989).

The use of ontogenetic features requires particular caution, because structures that appear homologous on the basis of pattern conformity are not always achieved along identical differentiation pathways (Dohle, 1989). Wagner (1989: 1163) addresses this problem in the framework of his "triple agenda of a biological homology concept: conservation, individuality, and uniqueness"; he states: "To explain these three properties of homologs, not all aspects of development are equally important. The source of cells seems to be irrelevant, as long as they interact in a coherent and conservative manner to produce a certain part of the body".

THE RELATIVE AGE OF HOMOLOGOUS CHARACTERS

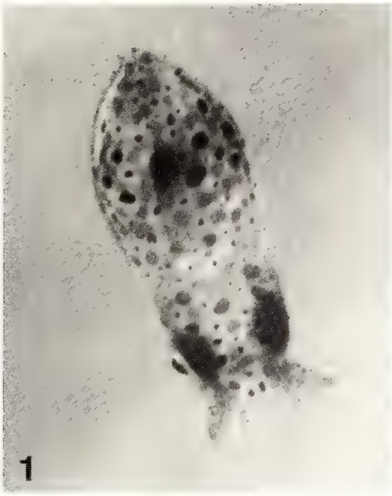
The recognition of homologies inevitably raises the question of the phylogenetic age of a character: when did character X first appear? In other words: when did this character become phenotypically stabilized in a population (representing an incipient species) which we can consider the ancestor of the species that still carry this character?

On the basis of paleomorphological data derived from the fossil record of cephalopods, we can 'reconstruct' more or less realistic paleobiological scenarios, but nothing in the fossil record provides direct evidence for any behavioral character that we observe in the living animals. So we depend *entirely* on the comparative analysis of behavior in living cephalopods when we deal with the question of what is 'primitive' and what is 'derived', and we are compelled to use the analytical approach employed by neontologists studying phylogenetic systematics based on morphological features. We seek the hierarchical arrangement of monophyletic groups, each defined by shared derived (synapomorphic) characters inherited from the direct common ancestor, and this implies that the homology hypothesis has been tested seriously for each of these characters. In this hierarchical arrangement, autapomorphic characters or character states assumed to mark an ancestral species are recognized as synapomorphic only in the immediate descendants; such characters 'become' symplesiomorphic (shared primitive) features as soon as one of these direct descendants is considered as the ancestor of a group of descendants of its own, so that new characters (different from the now symplesiomorphic ones) must be used to define that sub-group. A 'general pattern' of behavior can thus represent a symplesiomorphic character when a distinct 'variant' of the pattern appears as a synapomorphic character allowing definition of a monophyletic group. In other words, the 'chronological table' is reset for each character at a precise point of the 'transformation' line.

It would of course be helpful if we could use the 'chronological table' of ontogenetic development as an indication of the historical sequence of events. However, 'recapitulation' turns out to be rather incomplete due to the relative independence of the different morphogenetic timetables within organisms which results in heterochronic shifts through evolutionary time. The temporal order of the ontogenetic appearance can be disturbed in particular by size differences. For example, in young loliginid squids, the lateral spreading of the tentacles during hovering is the ontogenetically earliest arm display (Fig. 1); the fact that it appears earlier (in fact soon after hatching) in *Sepioteuthis sepioidea* (Blainville) than in *Loligo vulgaris* Lamarck does not mean that one situation is more 'primitive' than the other. The difference is apparently related to the size difference of the hatchlings, *S. sepioidea* being ontogenetically more 'advanced' due to the larger size of the egg from which it has hatched.

From the early tentacle display, a variety of V-shaped tentacle and arm postures develop during juvenile life, and here we finally observe what could be a truly apomorphic variant in *Sepioteuthis sepioidea*. In contrast to the other forms of V-shaped postures in which "the left and right groups of arms are separated" (Moynihan and Rodaniche, 1982: 77) and "can point forward, upward, or downward", the so-called Split posture is asymmetrical: "The arms are spearated to left and right as in simpler V's, but one side is pointed upward while the other side is simultaneously pointed downward". In contrast, a V-shaped arrangement of the arms pointed forward is so generalized in swimming or hovering cephalopods (including octopodids in slow backward swimming) that it seems rather difficult to single out a distinct variant of *symmetrical* spreading, apart from the question whether the underlying 'general pattern' is really homologous.

Although the recognition of homologous characters of behavior can be very difficult across higher taxa, an apomorphic character will still be discrete if it is not the variant of a generalized pattern concerning the whole arm crown. A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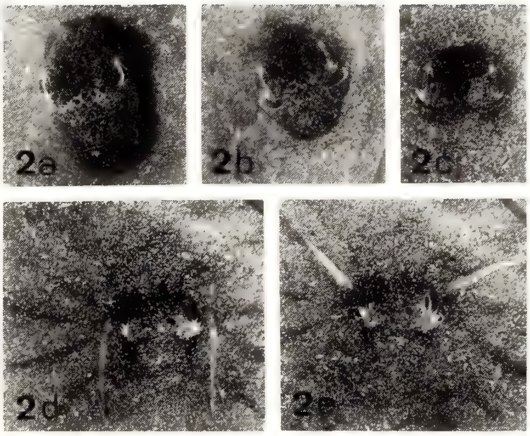

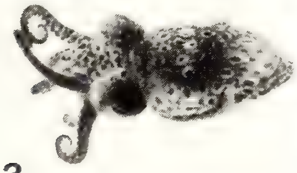
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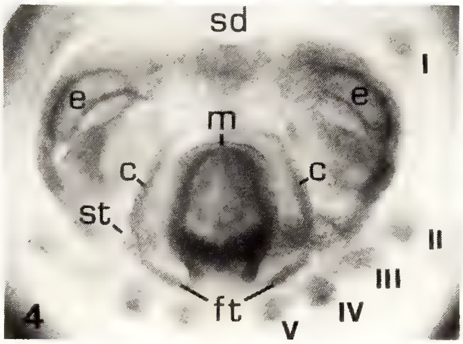

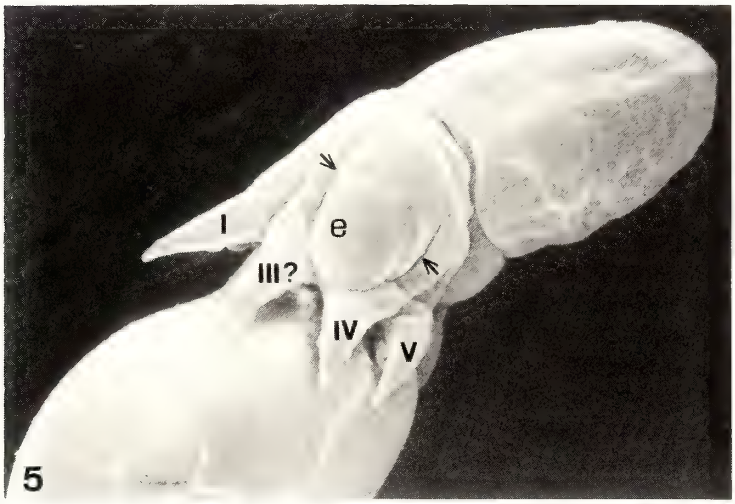

Fig. 1. *Loligo vulgaris*, one month old, hovering with tentacles spread, seen from the water surface (total length = 15 mm). **Fig. 2.** *Sepietta neglecta*, adult, covering itself with sand: **a,** the animal sits on the substratum, the arms are held under the head; **b,** the animal is now half-buried due to the action of the funnel (jets of water directed alternatingly forwards and backwards have 'fluidized' the sand surface momentarily, so that the animal 'sinks' into it); **c,** the animal at the end of the first burying phase, covered nearly entirely; **d, e,** second phase characterized by 'sand gathering' achieved by the dorsolateral arms (arm II). Note the traces of this arm action on the sand surface (total length = 30 mm). **Fig. 3.** *Sepietta obscura*, subadult, hovering with arm display. Note dorsolateral arms raised and curled, and ventolateral arms spread downwards with tips curled (total length = 50 mm). **Fig. 4.** Light micrograph of apical view of a living embryo of *Sepia officinalis* at stage IX of Naef (1928) showing organ rudiments as dark structures lying on the yolk mass. Around the central palleovisceral complex with the mantle (m) and collar (c) lie the eye (e) and stomodeum (sd) complexes and the paired rudiment of the funnel tube (ft); the latter has just separated from the arm rudiments V and becomes connected with the collar above the statocyst (st). Note the distance between arm rudiments I and II, and the inconspicuousness of arm rudiment IV from which the long tentacles are formed during subsequent stages (field width = 5 mm). **Fig. 5.** Post-organogenetic stage of *Octopus vulgaris* (preserved specimen in lateral SEM view , field width = 1.6 mm); the outer yolk sac (below) is only partly visible; the arms are numbered according to the homology hypothesis presented in this paper; the bases of the lateral arms reach around the eye (e) and form the folds (arrows) from which the primary lid is made at subsequent stages.

striking example is the special action of one pair of arms in a precisely defined situation in two sepiolid subfamilies, the Rossiinae and the Sepiolinae. These animals bury themselves in sand during daylight hours, as do other benthic cephalopods such as *Sepia*. The main work involved in sand covering is achieved by blowing up the substratum particles from underneath the body by water jets from the funnel (with vigorous fin movements counteracting the locomotory effect of the funnel jets). In contrast to *Sepia*, which finally smoothes the sand cover by a few rapid contractions of the dorsal mantle skin, all the benthic sepiolids studied thus far show a very peculiar 'second phase' in sand covering: the dorsolateral arms (Fig. 2) are stretched out to about the double normal length and again retracted and partly coiled in a sweeping movement by which sand particles are drawn to the head; this movement is repeated many times in all directions around the head (Boletzky and Boletzky, 1970). This strictly symmetrical pattern of highly sterotyped arm movements clearly represents a synapomorphic character of the Rossiinae and the Sepiolinae. In the third sepiolid subfamily, the pelagic Heteroteuthinae, such a movement pattern proper to the dorsolateral arms is not known. If it is indeed absent, it could a) have been secondarily suppressed; b) have been transformed into an autapomorphic variant; or c) have never existed. Evidence for 'c' would have to come from other characters indicating that the Heteroteuthinae form an 'outgroup' (i.e. stem from an ancestral form older than the common ancestor of Rossiinae and Sepiolinae). Whatever the answer, it must be emphasized that this peculiar action pattern is fully 'compatible' with the participation in other actions where the dorsolateral arms play a less spectacular role, especially during certain arm displays (Fig. 3; cf. Mauris, 1989). In other words, when the apparently 'new' program for the particular actions of the second arm pair in sand covering was assembled in the ancestral form (for which we have no age indication), it had to be integrated in a set of other programs already existing and functioning.

BEHAVIORAL HOMOLOGIES AND NEURAL PATHWAYS

Packard and Hochberg (1977: 226) present figures of the strikingly similar arm display called 'flamboyant' in a young octopus and in a young cuttlefish. They (op. cit.) raise the question: "If these patterns are considered homologous one with another, then what is the status of homology? It is not strictly a morphological one" (p. 225). They suggest: "Perhaps we should look upon them as behaviourally homologous - i.e. that they have the same behavioural origins", and they indicate what that implies : "If the selective advantage is in the behaviour itself, then natural selection may be relatively indifferent to the details of the means by which it is produced - so long as the means are effective" (p. 227). This proposition comes very close to what has been mentioned earlier concerning the "source of cells"that seems to be irrelevant "as long as they interact in a coherent and conservative manner to produce a certain part of the body" (Wagner, 1989: 1163).

The question then is whether behavioral homology can still be defined like a physical structure ("a certain part of the body"), or whether one could as well be dealing with similar patterns that have evolved *independently* using homologous effector systems, a special case of convergence called 'homoiology' (Lorenz, 1978; Tembrock, 1989). Although Packard and Hochberg (1977: 228) do not address explicitly this question, it is dismissed implicitly by their statement that "patterns are not a matter of a single set of elements or structures, but of all of them working together - in the skin, in locomotory structures and in modes of action - and given coherence by the brain. It is the repertoires read out from the central nervous programmes that have been selected in evolution". Ultimately then, behavioral homology should be expressed in the 'directions for use' rather than in the 'circuit diagram' of the nervous system. But so far we have access only to the 'circuit diagrams' which are so complex that they defy our capacity to sort out structural homologies at that level. Nonetheless, the comparative studies on the central pathways of the brachial nerves in decapods and octopods (Budelmann and Young, 1985, 1987) show the great potential of morphological analysis of the nervous system building on comparative studies that deal with the general correlations between brain structures and functional adaptations to ecological contexts (Young, 1988). It thus becomes - at least theoretically - possible to map all the neural connections between the periphery of the effector systems and sensory structures and the higher integration centers. Based on the results of centripetal cobalt filling of the brachial nerves of the third arm in *Sepia* and *Loligo*, Budelmann and Young (1987: 349) observe "a general similarity to the organization found by fillings of the brachial nerves of octopods, but with some differences (Budelmann and Young, 1985)". As in *Octopus* also the third arm was used to allow comparison, and considering that in the decapod species "differences may exist... for the pathways of the tentacle nerve" (Budelmann and Young, 1987: 346), the question of the morphological homology between the decapod tentacle and the third arm of octopods (Naef, 1928) becomes interesting. The hypothesis of homology between these arms in decapods and octopods can be tested on the basis of structural properties and positional relationships, but the latter must take account of certain devlopmental features.

DEVELOPMENTAL MORPHOLOGY OF THE COLEOID ARM CROWN

In morphogenetic terms, the arm crown of cephalopods arises from a paired series of embryonic cell concentrations that lie on either side of the body and head anlage. The situation of an early organogenetic stage of a cephalopod embryo is best visualized when one is looking from the animal pole along the main egg axis (i.e. in apical view); the arm rudiments then appear as a series of knobs arranged in two curved bands (Fig. 4). At their posterior end these bands approach one another close to the sagittal plane, whereas the anterior ends of the anlage lie far apart, forming a roughly U-shaped complex. It is subdivided into the individual arm rudiments ('knobs' or 'buds'), five on either side in decapod embryos, four in octopods. From the inner end of the posterior arm rudiments (close to the bottom of the U), a paired streak splits away to form the folds from which the funnel tube will be made (Naef, 1928). The common morphogenetic origin of the arms and the funnel tube (the funnel pouch or collar having a different origin) is also demonstrated by the close connection of the ganglionic masses forming the brachial and pedal lobes, from which the cerebral ganglion (forming the supraoesophageal parts of the brain) are clearly separated (Marquis, 1989).

The further differentiation of the four or five pairs of arm buds is characterized by the formation of small surface folds on the lower side of the arm (facing the outer yolk sac of the embryo) from which suckers differentiate. Along with the increase of arm length, the whole crown progressively contracts so that the open end of the U closes above the invaginated buccal mass. The resulting ring shape of the arm crown base forms the virtually radial arrangement of the arms from late embryonic stages.

During arm growth at advanced organogenetic stages, two pairs of folds form on the aboral side of the arm crown base (i.e. opposite the suckered arm face). One pair rises from the bases of the arms that are adjacent to the posterior arms (from which the funnel tube rudiments have split), the other pair of folds arises from the bases of the following arms. In the apical view considered up to now, these folds are seen to grow upwards, the first mentioned pair behind the eye, the second in front of the eye. In contrast to this so-called morpholocial (or embryological) orientation, the so-called physiological orientation considers the embryo in an orientation resulting from a 90° rotation backwards, so that the arms come to lie anteriorly, the funnel tube below ('ventrally'), and the mantle tip posteriorly. The two pairs of folds described above then appear to grow backwards around the eye complex (Fig. 5). The lower fold is the one arising from the base of the arm which can now be called ventrolateral, the upper fold arises from the lateral or dorsolateral arm of each side. These folds form the 'primary lid' which delimits the future orbital cavity surrounding the eye; they are the most important morphological markers for the recognition of arm homologies in coleoid cephalopods!

Among the criteria allowing one to recognize homologous structures, positional relationship is crucial (Remane, 1952; Riedl, 1978). It has been mentioned above that clearly homlogous structures are not always differentiated along strictly identical pathways. However, if one observes similar morphogenetic processes leading to the differentiation of organs that appear homologous on the basis of other criteria, and especially if there is not a single exception available to question the morphogenetic similarity, then the hypothesis of homology is greatly reinforced by that similarity. This is exactly what the arm crown development in coleoid embryos tells us about the homology of arms.

Unfortunately, the picture is blurred by the conventional numeration of arms in decapods and octopods. By excluding the tentacles from the numbered series of arm pairs, one unnecessarily obscures arm homologies. On the basis of the primary lid development, Naef (1928) emphasized that the tentacles of decapods and the ventrolateral arms of octopods are homologous (hence also the ventral arms in both groups). For the homologies of the lateral or dorsolateral, and of the dorsal arms, Naef suggested that arms II and III of decapods and arms I and II of octopods are homologous based on the argument that the dorsal arm rudiment in decapod embryos tends to lie removed from the dorsolateral bud II in early organogenesis (Fig. 4). But this hypothesis is ruled out by the positional relationship between the arm rudiments and the so-called meta-brachial vesicles; these are formed from two pairs of ectodermic invaginations, the dorsal pair lying between the bases of dorsal and dorsolateral arms in decapods and in octopods. Unless positional relationshps between the arms and the vesicles have changed (which is highly unlikely), the position of the dorsal pair of vesicles demonstrates the homology between the second (dorsolateral) octopodan arm pair and either the second or third arm pair of decapods (Boletzky, 1978-79). Loss of the second arm pair in the octopodan ancestor is suggested by the arm crown morphology of *Vampyroteuthis*, in which the second of a total of five arm pairs is rudimentary (forming the retractile filaments). This peculiar cephalopod probably represents a lineage from which the octopodan line became separated (see Young, 1977; Bandel and Boletzky, 1988). There is no direct morphogenetic evidence that it is actually arm II that is missing in octopods, because theoretically the dorsal fold of the primary lid could have been taken over by the second arm if formation of the arm III had been suppressed. In conclusion, there is good evidence of homology for the dorsal, ventrolateral (or tentacle), and ventral arms, respectively; and there is the acceptable hypothesis of absence of arm II in the octopods.

What remains to be discussed is the problem of buccal arm homology. Among the "general cephalopod features" Naef (1928: 82) described the division of the brachial complex into an "outer crown of tentacles and an inner one of buccal arms (Buccaltrichter) which surround the mouth as a third lip; they are more or less rudimentary in the dibranchiates'' (whereas they are known to form a well-developed complex in *Nautilus*). Naef emphasized that the buccal arms appear very late in decapod development (his detailed description of *Sepia* development is very conclusive) and interpreted the absence of buccal arms in octopods as the result of complete suppression. Given the positional relations between the 'outer crown' and the funnel tube, on the one hand, and with the primary lid, on the other (to which we can now add the position of the metabrachial vesicles), it would indeed be difficult to consider the octopodan arm crown as non-homologous to the 'outer crown' of decapods. This non-homology is actually proposed by Zell (1988: 87) who concludes from his analysis of adult characters that ''in all probability, the arms of ocotopods are not homologous to the sessile arms and tentacles but to the buccal arms of the decapods ''. His main arguments are structural resemblances in the muscle arrangement. Positional relationships of arms and buccal arms relative to the mouth are discussed without any reference to the developmental aspects described by Naef (1928) and more recent authors (see Boletzky, 1978-79 for literature).

ARM FUNCTIONS AND DEVELOPMENTAL CONSTRAINTS IN EVOLUTION

Considering that decapodan and octopodan arm crowns are probably homologous, and that within these arm crowns one can recognize arm identities at five positions in decapods and at four positions in octopods (with well established homologies for three of these positions), it becomes possible to approach the respective roles played by the different arms. To be exhaustive, a list of the functions of individual arm pairs would have to take account of variations due, for example, to the presence or absence of an interbrachial membrane, or its varied extension achieved by muscular action. Or when dealing with prehensile function in predation, mating or egg laying of oegopsid squids, the presence or absence of transformed suckers (hooks) would have to be specified. And wherever arm extension, spreading or curling appears to play a visual role in intra- or interspecific interaction, the question of concomitant effects outside the signal function would have to be considered. Needless to say, such a complete list of possibilities cannot be provided now. To reach that goal it will be necessary to take account of the developmental morphology of individual arm pairs, because group-specific modifications in the late embryonic 'programs' have set the stage for functional specialisations in arm crown evolution.

Let us consider the decapod tentacles (modified arms IV) from this point of view. In all decapods, with one exception as far as is known, the tentacle rudiments grow to a size at least equal to the size of other arms in the hatchling, and they immediately serve in prey capture. In the ommastrephid squids (where the arm buds III and V are 'retarded' in early development) the tentacle rudiments are drawn together at late embryonic stages, and they become fused to form a 'proboscis' carrying suckers at the anterior end which represents the rudimentary tentacle clubs. The subsequent juvenile development culminates in the progressive separation of the two tentacles (see Okutani, 1987 for a review). The transitory fusion can be viewed as the result of an evolutionary optimisation process in the line leading to the ommastrephid ancestor; after all, the separate adult tentacles can be joined at the club base during tentacle ejection in adult ommastrephids! On the other hand, instead of invoking a progressive displacement of an adult character to early ontogenetic stages, one might envisage a developmental constraint as possible cause; it could have been the small embryo size that switched morphogenetic 'canalization' over to a new route which proved adaptive.

It is interesting that the sole exception among decapods where tentacles are differentiated only during post-embryonic development is found in the pygmy cuttlefish *Idiosepius*, which produces very small eggs. In contrast to the ommastrephid embryo where the tentacles are fully formed (though fused) while two other arm pairs are retarded, *Idiosepius* forms all the 'sessile' arms during embryonic development, while the tentacle rudiments remain arrested at the early bud stage. This means that in very young *Idiosepius* prey capture must be achieved by the other arms, in a way similar to the prey capture in planktonic young octopuses (pouncing attack). When the tentacles of *Idiosepius* have grown to full length, they apparently serve in prey capture; however, in the adult female they are also used during spawning, to stick the eggs to the substratum (Natsukari, 1970). In all other decapods it is one or several other arms that fulfill this special prehensile function.

This observation finally raises the question of tentacle functions other than seizure of prey. Is the *Idiosepius* female really unique in using the tentacles for something other than feeding? Certainly not; it is apparently unique only in having tentacles participate in spawning. Moreover, this action appears as *reverse* prehension when compared to prey capture: instead of seizing prey with extended tentacles, then retracting the tentacles and releasing the prey item to the sessile arms (Kier, 1982, 1985), the *Idiosepius* female receives the egg expelled through the funnel in her arms, then the tentacles seize the egg and finally extend to release it as soon as it sticks to the substratum (Natsukari, 1970) (Fig. 6).

Apart from this peculiar behavior pattern, it has been said already that tentacles can participate in various arm displays in squids (Moynihan and Rodaniche, 1982; Hanlon, 1988; Porteiro *et al.*, 1990), even in very young animals (Boletzky, 1987). In these instances, no prehensile action

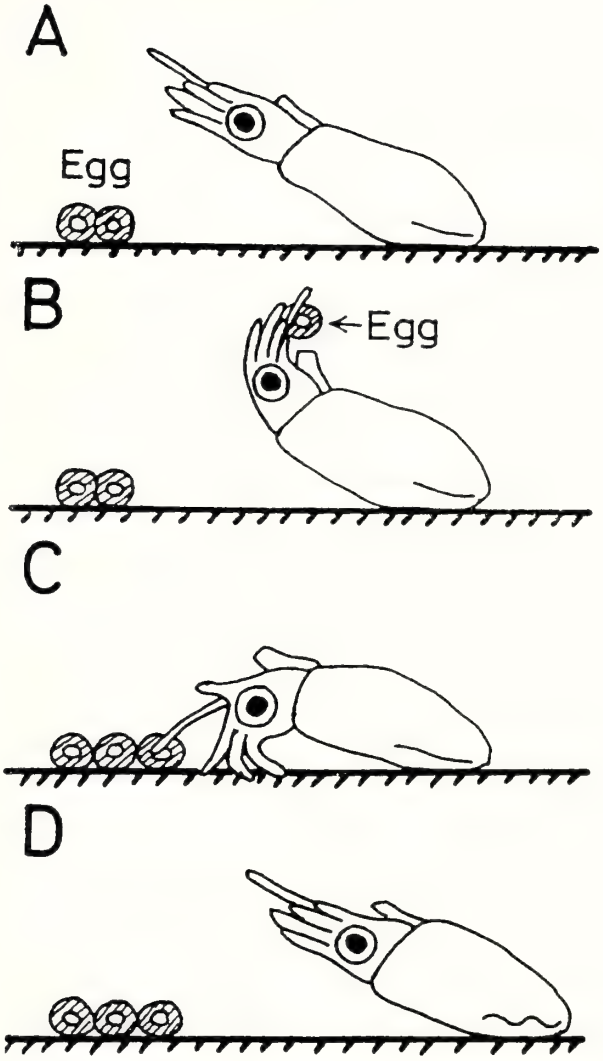

Fig. 6. A semi-schematic presentation of egg laying in *Idiosepius pygmaeus paradoxus:* **A,** the female is attached with its dorsal adhesive organ to the hard substratum (tank wall), close to eggs previously laid; **B,** an egg expelled through the funnel is seized with the tentacles; **C,** the egg is fixed to the substratum by the tentacles; **D,** the female moves a short distance in preparation for the following egg deposition (from Natsukari, 1970).

occurs. What is more intriguing is the fact that prehensile tentacle action may not occur during feeding. Very young *Sepia* always use their tentacles in prey capture, but older individuals develop an alternative pouncing attack which is generally used for the seizure of slow moving prey animals (Messenger, 1968; Duval *et al.*, 1984). During the positioning phase (with binocular fixation) the animal makes a decision whether to use the tentacles or make a pouncing attack with the arms. This decision may be influenced by previous failure to catch a particular prey item (Boletzky, 1972). *Sepia* is special in that the tentacles when not in use are fully retracted in tentacle pouches; nevertheless, arm attacks without use of the tentacles occur also in *Loligo* (Kier, 1982) and in ommastrephid squids (Bradbury and Aldrich, 1969; Flores, 1983).

Considering all the data on tentacle development and function in decapods, it is reasonable to assume that the whole action pattern of 'tentacle shooting' in prey capture is inherited from an ancestor that had arm IV differentiated for rapid extension (Kier, 1982, 1985), the emphasis being on rapid, because slow extension occurs in the arms of both decapods and octopods! The 'fixation' of the tentacle program in early ontogenetic stages has been cancelled apparently only in the idiosepiid ancestor. Although we thus have good reason to consider the tentacle ejection complex (which is coupled with binocular fixation of the target) as a homologous, indeed synapomorphous character of decapods, there is no evidence as yet that the arm attack pattern (which is essentially defined by the 'negative' feature of tentacles not being used) of cuttlefish, loliginid and ommastrephid squids is also homologous. Here homology is a likely guess, but homoiology also is conceivable.

The inverse situation, with homoiology as the favored hypothesis and actual homology at best conceivable, appears when the octopods are included in the comparative consideration of tentacles. The enlargement of the ventrolateral arms in *Octopus defilippi* Vérany and related species of the 'Macrotritopus' group is very unlikely to represent a true homology, because no trace of this feature appears in the cirrate octopods and in *Vampyroteuthis*. This incidentally removes also the possibility of deriving the special 'prehensile' function of the incirrate hectocotylus from the decapodan tentacle function as it appears in prey capture.

CONCLUSIONS

In focusing attention on 'what the arms do' in cephalopod behavior, the foregoing discussion has somewhat artifically eliminated the integration of arm postures in visually effective 'body patterns' (cf. Fig. 3). However, this aspect has been extensively covered by Packard and Sanders (1969, 1971), Moynihan and Rodaniche (1982), Hanlon and Messenger (1988) and Hanlon (1988). These studies deal with colorful inshore species that can be observed by SCUBA divers, and that can also be kept in the aquarium. Some can even be reared under fully controllable situations.

With the development of deep-diving research submersibles, a new area has been opened for field observations of living cephalopods, improving the conditions of study compared to the earlier investigations using remote control cameras (Roper and Brundage, 1972). In the deep sea, color plays no major role. In the aphotic zone, the arms of cephalopods can take on visually effective signal functions only if they carry light organs. Arm length and movement patterns could thus be adapted to that particular role along with the functional integration of prey capture and swimming or hovering. To fulfill optimally these latter functions, an arm crown devoid of light organs could be structured differently. The cirrate octopods present a variety of examples emphasizing the integrated function of very long arms with an enormously developed interbrachial membrane, which can become subdivided into an outer web attached to the arms via a so-called intermediate web (see Voss, 1988 for a review). However, the juveniles of these forms start out with very different body proportions including especially short arms and very large fins (Boletzky, 1982). Moreover, these short arms are still devoid of the cirri, so that the suckers alone must achieve what suckers and cirri do in the adult.

These are just a few aspects to which attention should now be drawn. An equally interesting field is the functional morphology of the outer and inner arm crowns of *Nautilus* and the related behavioral features. *Nautilus* uses its numerous tentacles in ways similar to certain arm actions in modern coleoid cephalopods, the ancestor of which must have been characterized by an arm crown comprising only ten arms (Naef, 1928).

The guiding thread through comparisons between any of the examples of arm actions mentioned is the *attempt* to recognize homologies, because the assumption of homology always remains hypothetical. In some cases, the homology hypothesis proves very robust, especially when built on the observation of structural complexity and its ontogenetic formation. In other cases, superficial resemblances suggest homology but may not stand rigorous tests. This is the crux of many behavioral features, but when it comes to comparing arm actions, it is at least helpful to have an idea of arm homologies.

The comparative method provides slow but steady progress in understanding the 'natural history' of organisms. Robust hypotheses do not appear out of the blue. As Young (1977: 430) wrote in his 'phylogenetic considerations', the concluding section of a survey of 'Brain, Behaviour and Evolution of Cephalopods': "We are gradually learning how to piece the information together and to correlate it with studies of the structure and organization of the brain. Such knowledge, gained inductively, can be used, with caution, for deductions about the probable habits of species not yet investigated at sea".

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Reproductive anatomies of *Holospira* spp. (Gastropoda: Pulmonata: Urocoptidae) from Arizona and Sonora with a new subgenus and a new subspecies*

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Abstract. The reproductive systems of seven species of *Holospira* from Arizona and Sonora, Mexico are illustrated and compared. They exhibit four different morphologies based on the size, shape and arrangement of the penial complex and the spermathecal duct. These four morphological groups represent lineages that do not completely correspond to the three presently recognized subgenera from this region.

Sonoraloa Gilbertson subg. *nov.* and *Holospira dentaxis alamellata* Gilbertson, ssp. *nov.* are described. *H. remondi* (Gabb, 1865), *H. dentaxis* Pilsbry, 1953 and *H. mazatlanica* (Bartsch, 1943) are transferred from subgenus *Allocoryphe* to *Sonoraloa*.

Land snails comprising the urocoptid genus *Holospira* von Martens, 1860, exhibit moderate-sized (ca. 8-20 mm in length), elongated, turriform shells that retain their spire. They inhabit three southwestern states (Arizona, New Mexico, and Texas) and range southward through most of Mexico. Most species are very xerophytic and calcicolous. Three of the six subgenera recognized presently [*Allocoryphe* Pilsbry, 1946; *Eudistemma* (Dall, 1896); and *Holospira s.s.* von Martens, 1860] are represented in Arizona and Sonora, Mexico, the northwestern corner of the *Holospira* range.

The taxonomy of the genus is based entirely on shell characteristics such as overall size, whorl size, shape of the aperture, sculpture and aspects of the internal column. However, these characters tend to be somewhat unreliable for systematic studies due to their variability. Thompson (1964) suggested that true interspecific relationships within the genus are best determined by the soft anatomy. Unfortunately, holospiras are poorly known in this regard. Descriptions of the reproductive systems of only a few species (11) have been published (Pilsbry, 1903; Gilbertson, 1989a, b; Thompson, 1964). Five of these are from Arizona and Sonora, Mexico (Gilbertson, 1989a, b).

The present paper describes the reproductive anatomies of three additional *Holospira* species from Arizona and two from Sonora. The anatomical configuration of the soft parts of the two Sonoran species, along with aspects of the embryonic whorls of their shells, indicates a separate lineage which requires the description of *Sonoraloa* subg. *nov.*

MATERIALS AND METHODS

Estivating snails were collected from under surface rocks and/or dead plant material (especially agaves and yuccas) usually in areas of limestone deposits. The Mexican species were collected at sites in central Sonora, between Hermosillo and Sahuaripa (Fig. 1), including the Sierra Batamote. In Arizona, collections were made in the Dragoon and Huachuca Mountains.

Mature specimens were immersed individually in a small vial of water for three to five days until drowned. The shell of each specimen was broken and removed carefully. Then the reproductive system of the animal was dissected free from the other internal organs and fixed in 70% ethanol. The reproductive organs were stained with Delafield Haematoxylin, destained with 3% acid alcohol, counter-stained with Eosin Y, and slide-mounted (see Gregg, 1959; Naranjo-Garcia, 1989). The reproductive systems of two to four specimens of each species were dissected and mounted.

Institutions cited in this article are abbreviated as follows: ANSP, Academy of Natural Sciences of Philadelphia; LACM, Los Angeles County Museum of Natural History; SBMNH, Santa Barbara Museum of Natural History; UNAM, Universidad Nacional Autonoma de Mexico; USNM, United States National Museum-Smithsonian Institution.

TAXONOMIC DESCRIPTIONS

Genus *Holospira* von Martens, 1860

Subgenus *Allocoryphe* Pilsbry, 1946

(Figures 2, 3a)

Type species: *Holospira (Allocoryphe) minima* von Martens, 1897, by original designation. The subgenus is monotypic.

Type locality: Cerro de la Campana, Hermosillo, Sonora, Mexico.

Diagnosis: Shell exhibits a rounded aperture, expanded

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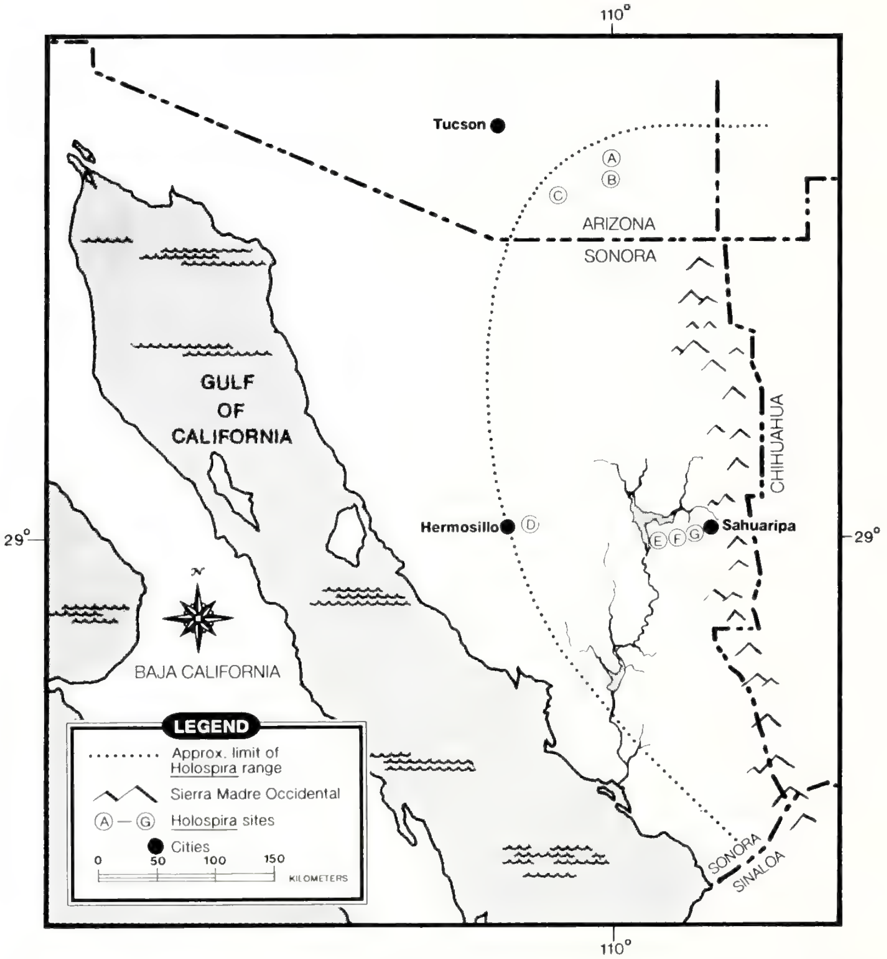
110°
Tucson
Ⓐ
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ARIZONA
SONORA
GULF OF CALIFORNIA
Hermosillo
Ⓓ
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Sahuaripa
CHIHUAHUA
29°
29°
BAJA CALIFORNIA
LEGEND
Approx. limit of Holospira range
Sierra Madre Occidental
Ⓐ — Ⓖ Holospira sites
Cities
0 50 100 150 KILOMETERS
SONORA
SINALOA
110°

Fig. 1. Map of Arizona and Sonora, Mexico showing approximate locations of collecting sites of *Holospira* spp. discussed in this paper. **A.** *H. (Eudistemma) tantalus campestris;* **B.** *H. (E.) danielsi;* **C.** *H. (E.) ferrissi;* **D.** *H. (Allocoryphe) minima;* **E.** *H. (H.) milleri;* **F.** *H. (Sonoraloa) remondi laevior;* **G.** *G. (S.) dentaxis alamellata* spp. *nov.*

peristome, hollow ribs and a somewhat enlarged, alamellate, internal column. Embryonic whorls flat-sided and angular at the upper, outer margin. Male anatomy with tubular epiphallus inserting laterally into penis producing a penial caecum. Penial retractor muscle broad, inserting on apex of penial caecum.

Material examined: ANSP 166366, Cerro de la Campana, Hermosillo, Sonora, 55+ shells. SBMNH 35519, Cerro de la Mona, ca. 21 km east of Hermosillo, Sonora, N side of Hwy 15, 29º02.9'N, 110º39.4'W, elevation ca. 350 m, shell and slide-mounted reproductive system (illustrated specimens). SBMNH 35626, Cerro de la Mona (as above), 8 shells. LACM 88-354.1, Cerro de la Mona (as above), 7 shells.

Remarks: Pilsbry (1946) erected the subgenus *Allocoryphe* (allo, different; coryph, top) in a footnote for the "special group" of holospiras inhabiting northwestern Mexico, between the Sierra Madre Occidental and the Gulf of California (Fig. 1). This subgenus is restricted herein to *Holospira minima*, which is the only *Holospira* species known to exhibit angular, embryonic whorls (i.e. a "different top"). These whorls are sculptured with "regularly spaced ribs that are overlayed by an open mesh of granular reticulations" (Thompson, 1988:92).

Subgenus *Sonoraloa* Gilbertson subg. *nov.*

(Figs. 3c, 4, 5, 6, 7)

Type species: *Holospira remondi* (Gabb, 1865), designated herein. *H. remondi, H. dentaxis* Pilsbry, 1953, and *H. mazatlanica* (Bartsch, 1943) are transferred from subgenus *Allocoryphe.*

Type locality: 1.5 leagues (ca. 6 km) from Arivechi, Sonora, Mexico.

Distribution: Sonora and Sinaloa, Mexico.

Diagnosis: Shell generally similar to that of subgenus *Allocoryphe* with regard to aperture, peristome, and whorl size but differing by having one lamella (the axial), or none,

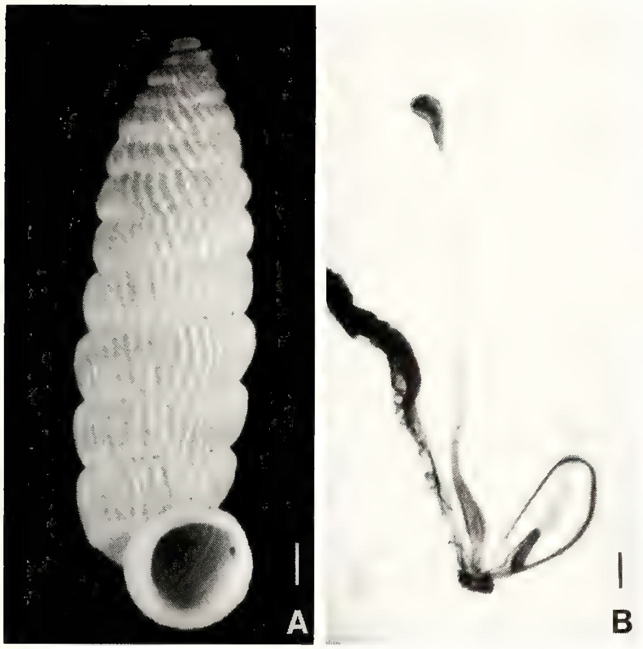

Fig. 2. *Holospira (Allocoryphe) minima.* **A.** Apertural view of shell. **B.** Reproductive system (except albumen gland and ovotestis) (scale bars = 1 mm).

on the internal column and having rounded, embryonic whorls. Male anatomy with a tubular epiphallus inserting apically on an ovate penis, adjacent to insertion of penial retractor muscle.

Material examined: ANSP 25046, *Holospira remondi*, 1.5 leagues (ca. 6 km) from Arivechi, Sahuaripe Valley, Sonora, one lectotype. ANSP 166484, *H. dentaxis*, drift at ford of Rio Yaqui about 17.5 km N of Ciudad Obregon, Sonora, holotype, 3 paratypes. USNM 381625, *H. mazatlanica*, drift at Mazatlan, Sinaloa, Mexico, 4 paratypes.

Etymology: *Sonoraloa* is a contraction of the names of the two northwestern Mexican states which comprise the known range of this subgenus, Sonora and Sinaloa.

Remarks: *Holospira dentaxis, H. mazatlanica* and possibly *H. remondi* (including numerous subspecies) were described on the basis of river drift shells. Because of this, it is very difficult to locate living populations. However, populations referrable subspecifically to *H. remondi* and *H. dentaxis* have been located and their reproductive anatomies are discussed herein.

Holospira kinonis Baily and Baily, 1940, is the only other species that Pilsbry (1953) placed in the subgenus *Allocoryphe*. However, its shell is very slender and turriform, giving it the external appearance of an *Epirobia*, and its embryonic whorls are rounded, but differ from those of the other species by not enlarging in diameter. Because of these shell features, and lack of anatomical data, its taxonomic status is uncertain.

Holospira (Sonoraloa) remondi laevior Pilsbry, 1953
(Figs. 3c, 7)

Synonym: *Holospira remondi* (Gabb, 1865)

Material examined: ANSP 188316, *Holospira remondi laevior*, drift of Laguna Preza Rodriguez, Hermosillo, Sonora, holotype, 3 paratypes. SBMNH 35520, *H. remondi laevior.* Sierra Batamote, east-central Sonora (near El Milagro Mine), ca. 1,070 m, 20.2 km E of Rio Yaqui Bridge along Hwy 15 from La Estrella to Bacanora, 28°57.7'N, 109°30.5'W, Sonora, shell and slide-mounted reproductive system (illustrated specimens). SBMNH 35603, *H. remondi laevior*, Sierra Batamote (as above), 5 shells. LACM 88-355.1, *H. remondi laevior*, Sierra Batamote (as above), 6 shells.

Remarks: The cylindroconic shells of the present population from the Sierra Batamote are slightly longer (mean length = 14.6 mm for 11 shells) than that of holotype *H. remondi laevior* (length = 13.8 mm) but overlap occurs (range = 13.4 - 17.0 mm). Their somewhat inflated internal columns (ca. 0.18-0.20 of shell width) suggest a close relationship with genus *Coelostemma* Dall, 1895.

Bequaert (1973) synonomyzed *Holospira remondi laevior* (and all other subspecies) with the nominate subspecies without comment. It is considered valid herein due to the characteristically elongated, cylindric portion of its shell.

Holospira (Sonoraloa) dentaxis alamellata
Gilbertson ssp. *nov.*
(Figs. 4-6)

Diagnosis: Shell comparable to *Holospira dentaxis dentaxis* Pilsbry, 1953, in overall shape, shape of the aperture, whorl size and sculpture but slightly larger and alamellate (holotype *H. d. dentaxis* is 11.0 mm in length, 3.5 mm in diameter, 13 whorls and has an axial lamella).

Shell of holotype: Shell medium-sized for genus, moderately cylindroconic in shape, convex with ninth whorl of greatest diameter, tan in color. Whorls very convex, 12.1 in number. Embryonic whorls 2.4 in number, rounded, minutely granular, increasing in diameter. All post-embryonic whorls sculptured with moderate-sized, solid, axial ribs which are slightly retractively slanted and arched, having intercostal spaces ca. three times width of ribs. Penultimate whorl with 31 ribs. Aperture slightly auriculate; peristome extended somewhat from body whorl and moderately expanded except on upper-outer margin. Umbilicus narrowly perforate. Internal column smooth, slightly expanded, increasing in diameter apically. Maximum length 11.7 mm, diameter 4.0 mm.

Paratypes: Seven paratypes vary from turriform to cylindroconic in shape. They range from 10.9 to 11.9 mm in length (mean 11.5 mm) and 3.7 to 4.0 mm in diameter (mean 3.9). Radula: Radula typical for genus. Formula 16-6-1-6-16 (= 45

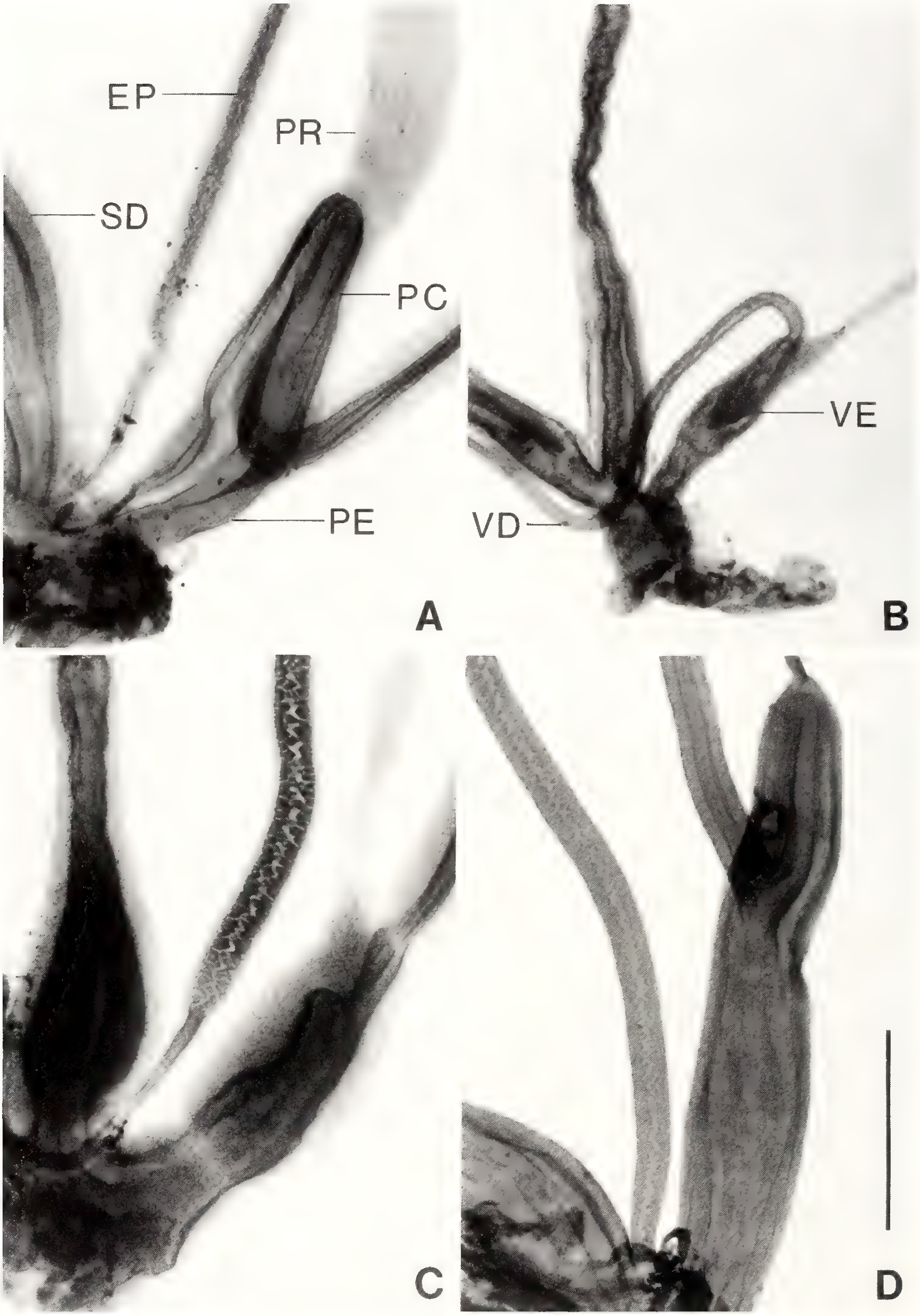

Fig. 3. Basal reproductive organs of *Holospira* spp. representing the four lineages discussed herein. **A.** *H. (Allocoryphe) minima.* **B.** *H. (Holospira) milleri.* **C.** *Holospira (Sonoraloa) remondi laevior.* **D.** *H. (Eudistemma) danielsi.* Abbreviations: EP, epiphallus; PC, penial caecum; PE, penis; PR, penial retractor muscle; SD, spermathecal duct; VD, vas deferens; VE, verge (scale bar = 1 mm).

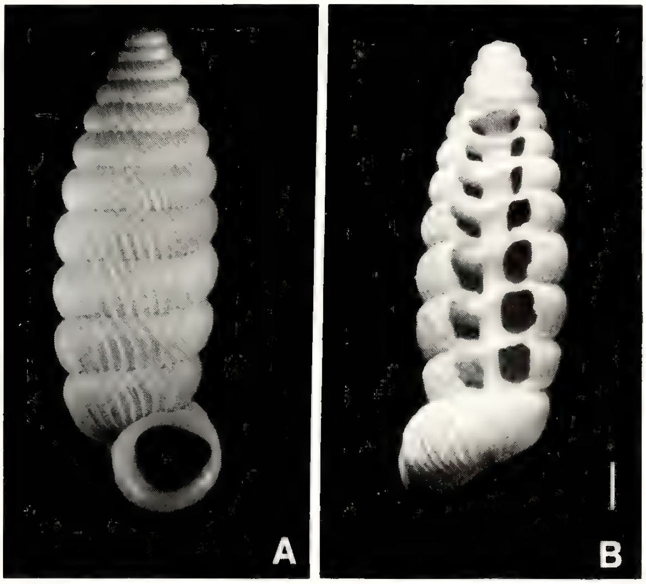

Fig. 4. *Holospira (Sonoraloa) dentaxis alamellata ssp. nov.* **A.** Apertural view of holotype. **B.** Dorsal view of paratype opened to show internal column (scale bar = 1 mm).

teeth per row).

Reproductive system: Penis small and slightly ovate due to a constriction at junction with genital atrium. Vas deferens enlarging into tubular epiphallus which inserts apically into penis. Spermathecal duct rounded basally with internal folds, proceeding apically into short constricted section, and then enlarging with scalloped-appearing interior; spermatheca tapering into duct. Spermathecal diverticulum lacking.

Type locality: Riperian gorge, S side of Hwy 15, 7.5 road km W of Sahuaripa, 29°01.5’N, 109°18.7’W, elevation ca. 700 m, Sonora Mexico.

Disposition of types: Holotype: SBMNH 35514. Paratypes: ANSP 389889; LACM 2246; UNAM-IB 190; USNM 860570. SBMNH 35515, slide-mounted reproductive system (illustrated specimen). SBMNH 35593, 35594, two slide-mounted reproductive systems.

Etymology: This subspecies is named for the absence of lamellae on the internal column.

Remarks: *Holospira dentaxis dentaxis* Pilsbry, 1953, *H. d. lamellaxis* Pilsbry, 1953, *H. d. striatella* Pilsbry, 1953 and *H. d. pomatia* Pilsbry, 1953 were described on the basis of drift shells from the mouth of the Rio Yaqui. Bequaert (1973) synonomyzed all subspecies with the nominate subspecies.

DESCRIPTIONS OF REPRODUCTIVE ANATOMIES

Holospira species inhabiting Arizona and Sonora, Mexico exhibit at least four distinctly different arrangements (= lineages) of the reproductive system based on variations of the male genitalia and the female spermathecal duct. Other female organs such as the free oviduct, uterus and albumen gland are morphologically similar, varying only in length. In all cases, the spermathecal duct is completely separate from the free oviduct; hence, a vagina is lacking. A spermathecal diverticulum is present in the Arizona species (lineage 1) and is lacking in all three of the Sonoran groups (lineages 2-4).

LINEAGE 1: Subgenus *Eudistemma* (Dall, 1896)

Holospira (Eudistemma) danielsi Pilsbry and Ferriss, 1915 (Figs. 8, 9)

Material examined: SBMNH 35516, foothills on N side of mouth of Cochise Stronghold Canyon West, Dragoon Mts., 31°56.0’N, 110°00.1’W, elev. ca. 1615 m, Cochise Co., Arizona (at or near type locality), one slide-mounted reproductive system (illustrated specimen). SBMNH 35595, 35596 (data as above), two slides.

Reproductive system: The male anatomy is characterized by

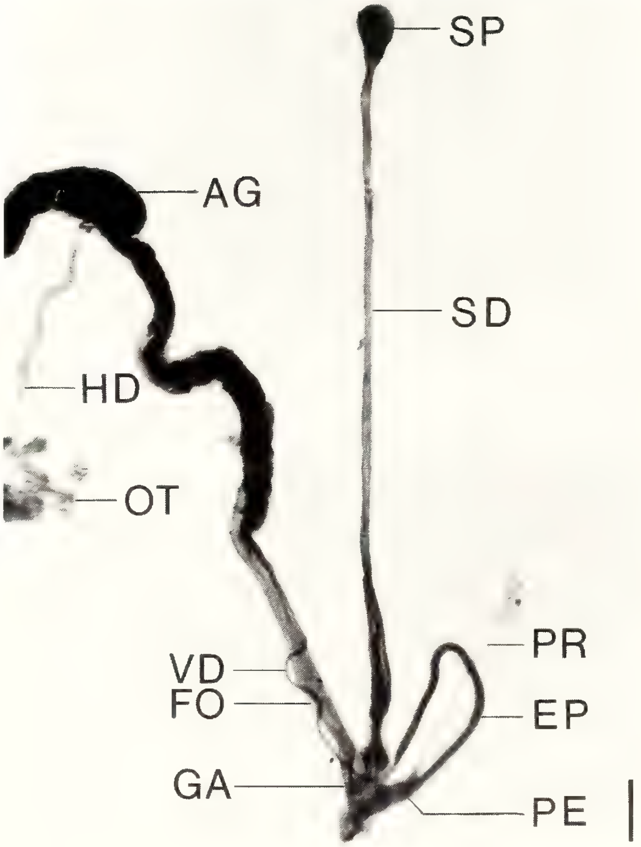

Fig. 5. Reproductive system of *Holospira (Sonoraloa) dentaxis alamellata* spp. *nov.* Abbreviations: AG, albumen gland; EP, epiphallus; FO, free oviduct; GA, genital atrium; HD, hermaphroditic duct; OT, ovotestis; PE, penis; PR, penial retractor muscle; SD, spermathecal duct; SP, spermatheca; VD, vas deferens (scale bar = 1 mm).

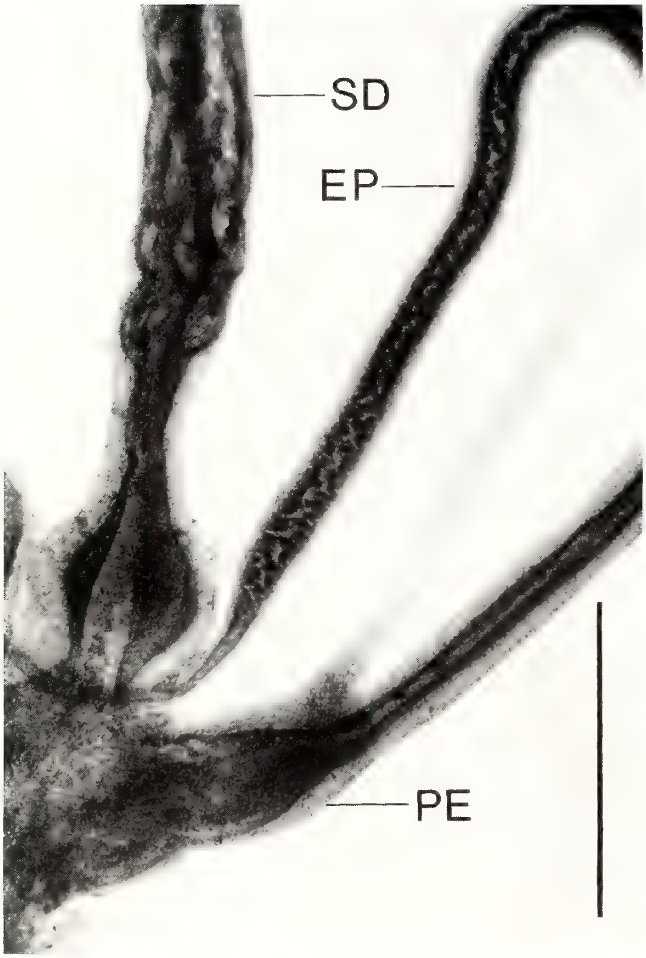

Fig. 6. Basal reproductive organs of *Holospira (Sonoraloa) dentaxis alamellata* spp. *nov.* Abbreviations: EP, epiphallus; PE, penis; SD, spermathecal duct (scale bar = 1 mm).

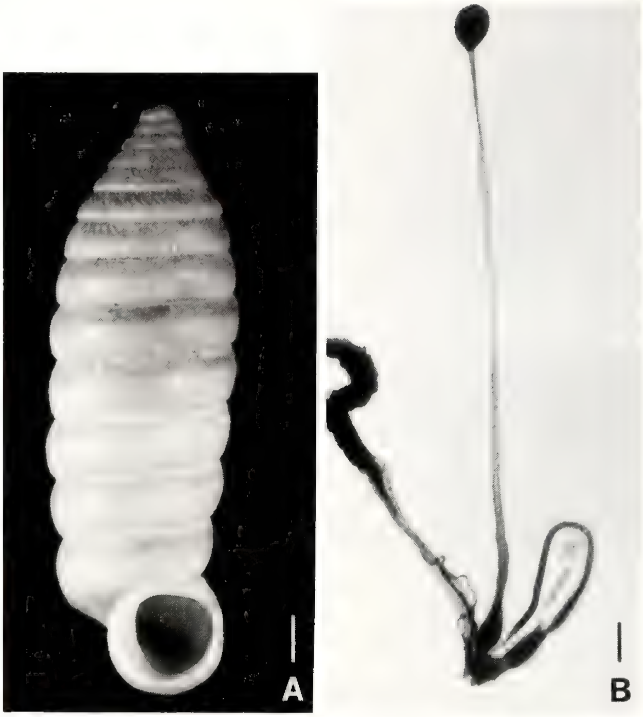

Fig. 7. *Holospira (Sonoraloa) remondi laevior.* **A.** Apertural view of shell. **B.** Reproductive system (excluding albumen gland and ovotestis) (scale bars = 1 mm).

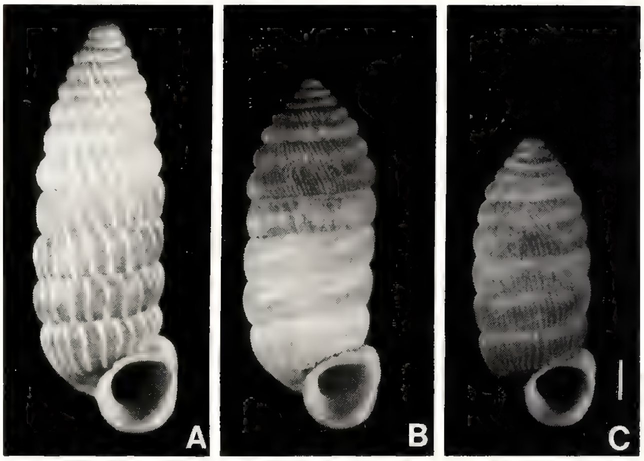

Fig. 8. Apertural view of three Arizona *Holospira* species. **A.** *Holospira (Eudistemma) danielsi.* **B.** *H. (E.) tantalus campestris.* **C.** *H. (E.) ferrissi* (scale bar = 1 mm).

an elongate penis which contains slight internal folds of tissue. The apical portion of the penis is a caecum due to the lateral insertion of the epiphallus. The epiphallus is an elongate (Appendix 1), tubular enlargement of the vas deferens which contains a serrate-appearing, glandular endothelium in its proximal portion. The penial retractor muscle is rather slender, and inserts on the rounded (dome-shaped) apex of the penial caecum. The spermathecal duct is characterized by a diverticulum and an elongate, gradually tapering spermatheca. A retractor muscle inserts on the basal portions of the oviduct and spermathecal duct.

Holospira (Eudistemma) tantalus campestris Pilsbry and Ferriss, 1915 (Figs. 8, 10)
Synonym: *Holospira campestris* Pilsbry and Ferriss, 1915
Material examined: SBMNH 35517, Wood Canyon near a rock quarry, NW end of Dragoon Mountains, 32°00.5'N, 110°00.2'W, elevation ca. 1640 m, Cochise Co., Arizona, one slide-mounted reproductive system (illustrated specimen). SBMNH 35597 (data as above), one slide.
Reproductive system: Similar to *H. danielsi* except: 1) the spermathecal duct is longer and more slender (including the base); 2) the epiphallus is longer and more slender; 3) the

apex of the penial caecum is tapered; 4) the penis lacks internal folds.

Holospira (Eudistemma) ferrissi Pilsbry, 1905 (Figs. 8, 11)
Material examined: SBMNH 35518, foothills immediately SE of Manila Mine, NW end of Huachuca Mts., 31º33.2'N, 110º26.2'W, elev. ca . 1620 m, Cochise Co., Arizona (type locality), one slide-mounted reproductive system (illustrated specimen). SBMNH 35598 (data as above), one slide.

Reproductive system: Similar to *Holospira (Eudistemma) danielsi* except that: 1) the system is smaller overall (ca. 0.70); 2) the basal portion of the spermathecal duct is distinctly rounded; 3) the apex of the penial caecum is tapered and; 4) the penis lacks internal folds.

Remarks: *Eudistemma* (see Bequaert and Miller, 1973:138) is the primary subgenus of *Holospira* in Arizona. It inhabits a small southeastern corner of the state and extends eastward through southern New Mexico into northwestern Texas. One population referrable to *H. (E.) ferrissi* Pilsbry, 1905 has been located in extreme northern Sonora (Bequaert and Miller, 1973).

Holospira (Eudistemma) danielsi, *H. (E.) ferrissi* and *H. (E.) tantalus campestris*, exhibit similar reproductive systems. The comparable systems of two other species in subgenus *Eudistemma*, namely *H. (E.) arizonensis* and *H. (E.) chiricahuana* Pilsbry, 1905, have been published (Gilbertson, 1989b). *H. arizonensis* has a slender (including the base), elongated (14.8 mm in the described specimen) spermathecal duct which closely resembles that of *H. tantalus campestris*. *H. chiricahuana* exhibits distinct undulated internal folds in the penis and lower spermathecal duct that are not apparent in the presently described species (nor in *H. arizonensis*). A retractor muscle inserting on the basal female structures is present in all species observed. The majority of the muscle was eliminated during dissection of the photographed specimens of *H. tantalus campestris* and *H. ferrissi*.

Holospira (Holospira) sherbrookei Gilbertson, 1989, from the Chiricahua Mountains, exhibits a reproductive system that corresponds with those of *Eudistemma* spp. It is placed in *Holospira s.s.* because of its quadrilamellate shell condition.

The *Eudistemma* reproductive system is somewhat comparable to that of snails in subgenus *Bostricocentrum* Strebel, 1880, from southern Mexico (Thompson, 1964). Snails in both subgenera exhibit a spermathecal diverticulum, an elongate spermatheca and a long, slender, tubular epiphallus. However, in *Bostricocentrum* the epiphallus inserts apically into the penis and the penis exhibits a terminal knob for the attachment of the retractor muscle.

LINEAGE 2: Subgenus *Allocoryphe* Pilsbry, 1946

Holospira (Allocoryphe) minima (Figs. 2, 3a)

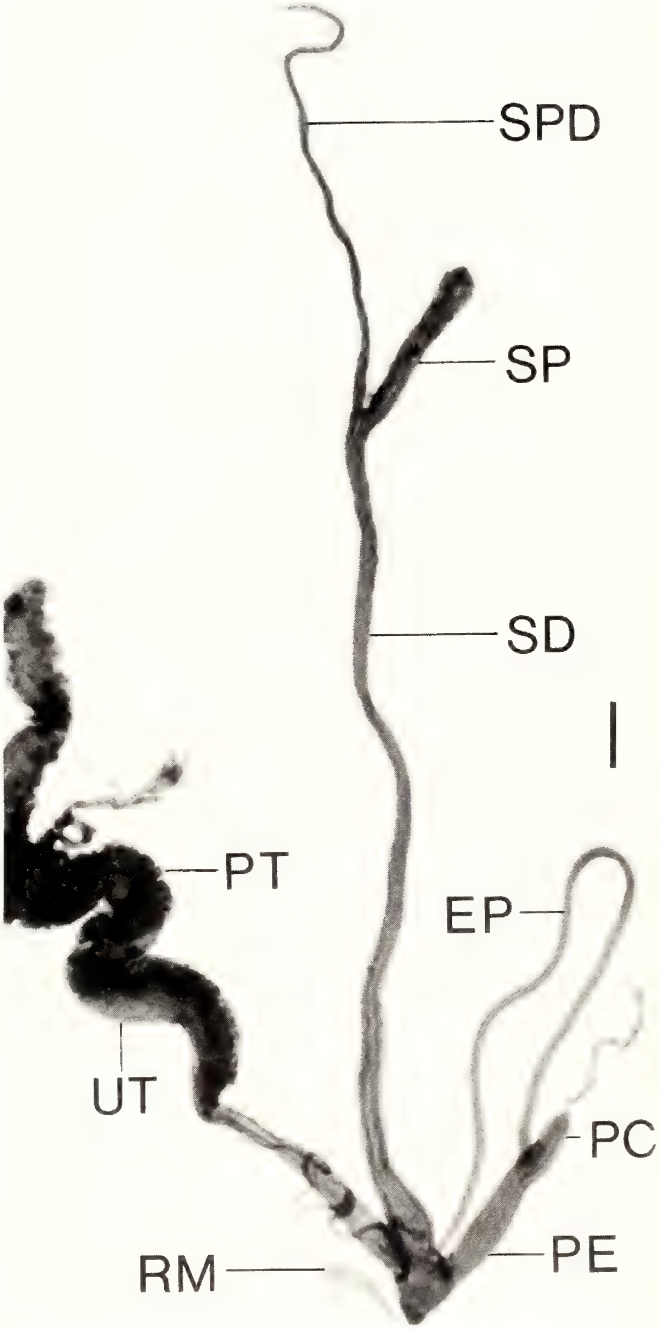

Fig. 9. Reproductive system of *Holospira (Eudistemma) danielsi* (except ovotestis). Abbreviations: EP, epiphallus; PC, penial caecum; PE, penis; PT, prostate gland; RM, retractor muscle; SD, spermathecal duct; SP, spermatheca; SPD, spermathecal diverticulum; UT, uterus (scale bar = 1 mm).

Material examined: SBMNH 35519, Cerro de la Mona, ca. 21 km east of Hermosillo, Sonora, N side of Hwy 15, 29º02.9'N, 110º39.4'W, elevation ca. 350 m, one slide-mounted reproductive system (illustrated specimen). SBMNH

35599, 35600 (data as above), two slides.

Reproductive system: The male anatomy is characterized by the presence of a stout, tubular epiphallus which inserts laterally into the penis producing an apical penial caecum. This caecum is ca. two-thirds of the total penis length and (along with the penis proper) contains internal folds of tissue. The penial retractor muscle attaches to the apex of the penial caecum and is unusually broad. The spermathecal duct is inflated basally and its spermatheca tapers into the duct.

Remarks: *Holospira minima* is the only species known to exhibit this morphology of the reproductive system. It appears to correlate with the presence of its distinctive, embryonic whorls.

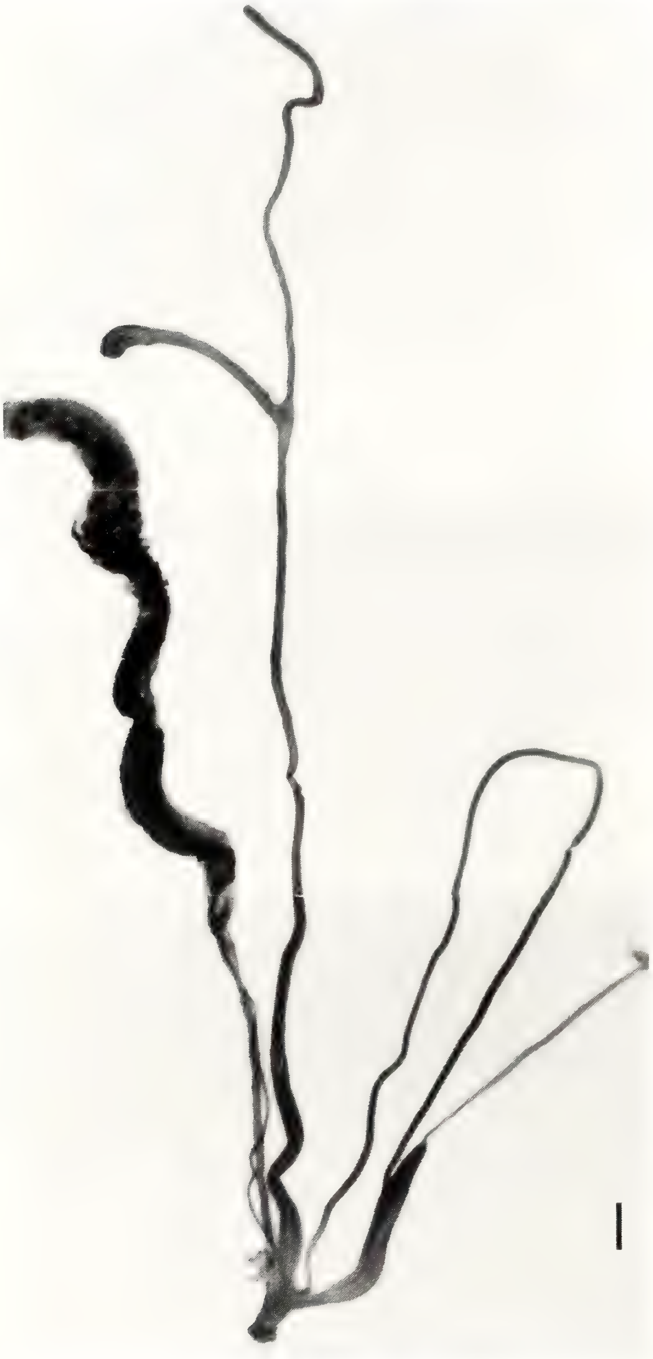

Fig. 10. Reproductive system of *Holospira (Eudistemma) tantalus campestris* (except ovotestis) (scale bar = 1 mm).

LINEAGE 3: Subgenus *Sonoraloa* Gilbertson, subg. *nov.*
Holospira (Sonoraloa) remondi laevior Pilsbry, 1953
(Figs. 3c, 7)

Material examined: SBMNH 35520, Sierra Batamote, east-central Sonora (near El Milagro Mine), ca. 1,070 m, 20.2 km E of the Rio Yaqui Bridge along Hwy 15 from La Estrella to Bacanora, 28°57.5'N, 109°30.5'W, Sonora, Mexico, one slide-mounted reproductive system (illustrated specimen). SBMNH 35601, 35602 (data as above), two slides.

Reproductive system: The male anatomy is characterized by a vas deferens that enlarges abruptly into a tubular epiphallus. It continues to enlarge distally before inserting apically into the penis. The penis is ovate, constricting at its junction with the genital atrium and exhibits a diagnostic internal outline. The penial retractor muscle is moderate in size, inserting apically onto the penis, adjacent to the epiphallus. The spermathecal duct is expanded basally (ca. same size as penis), and proceeds apically into an internally convoluted section; the spermatheca is oval-shaped.

Remarks: The penial complex of *Holospira (Sonoraloa) remondi laevior* is similar to that of *H. (S.) dentaxis alamellata* ssp. *nov.* They differ from the male anatomy of *H. (Allocoryphe) minima* by: 1) the apical insertion of the epiphallus into the penis, 2) the oval shape of the penis and 3) the narrower (ca. one-half to one-third width) penial retrac-

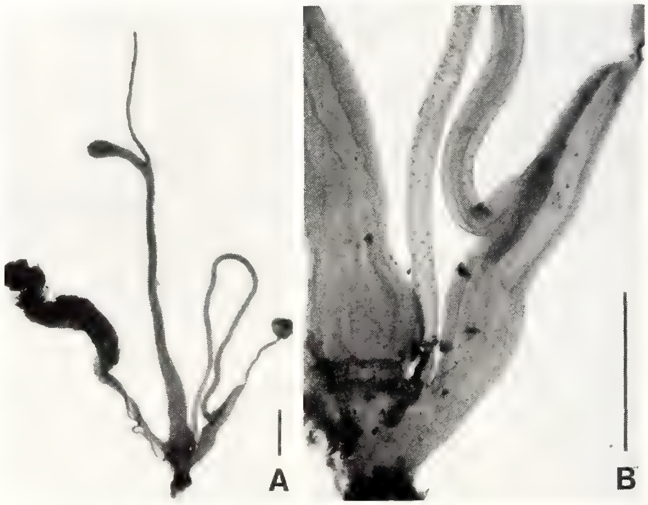

Fig. 11. Reproductive system of *Holospira (Eudistemma) ferrissi* (except ovotestis. **A.** Entire system. **B.** Basal anatomy (scale bars = 1 mm).

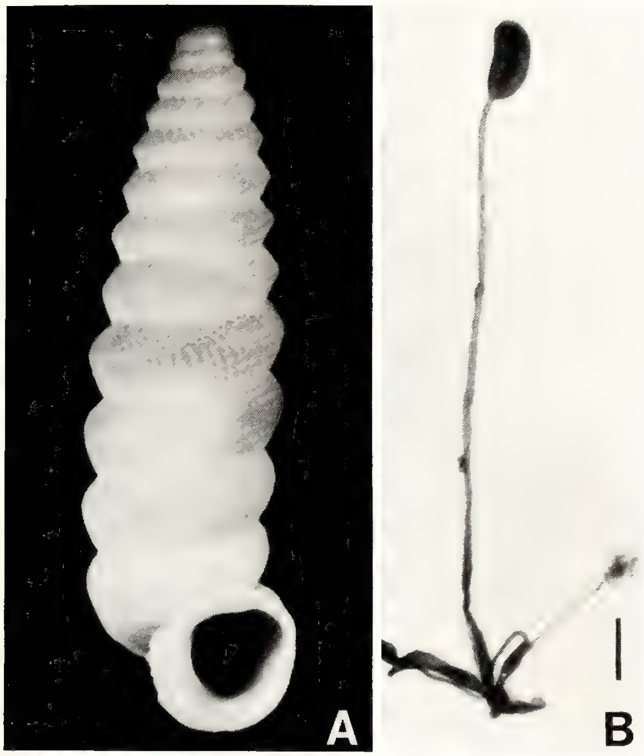

Fig. 12. *Holospira (H.) milleri.* **A.** Apertural view of shell. **B.** Male reproductive system and female spermathecal duct (scale bar = 1 mm).

tor muscle. These differences confirm the validity of *Sonoraloa* subg. *nov.*

LINEAGE 4: *Holospira s.s.* von Martens, 1860
Holospira (Holospira) milleri Gilbertson, 1989
Figs. 3b, 12)

Material examined: SBMNH 35521, E side of Rio Yaqui in a ravine near mouth of El Alamo Wash, ca. 1.5 km S of the military footbridge at El Novillo; 28º58.1'N, 109º37.5'W, elev. ca. 260 m, Sonora, Mexico (type locality), one slide-mounted reproductive system (illustrated specimen). SBMNH 35604, 35605, 35606 (data as above), three slides (two specimens possibly immature).

Reproductive system: See Gilbertson (1989a) for original description. The male system exhibits a small penial sac which contains a verge. The vas deferens inserts into a short, conic epiphallus atop the penial sac. The basal portion of the spermathecal duct typically contains an undulated, internal lumen although it is not seen on the illustrated specimen. The spermatheca is indented medially (reniform) and constricted basally before joining the spermathecal duct.

Remarks: The male anatomy of *Holospira (H.) milleri* is dramatically different from that of all other described *Holospira* spp. (for which the anatomy is known). It is the only species that exhibits a verge in the penial sac and whose vas deferens does not enlarge into a tubular epiphallus.

An undescribed ''form'' with a trilamellate shell was discovered at the same site as *Holospira (Sonoraloa) remondi laevior* in the Sierra Batamote. Its anatomy is very similar to that of *H. (H.) milleri* (including the presence of a verge). However, because of the trilamellate shell condition, this ''form'' cannot be included in *Holospira s.s.* (along with *H. milleri*) as the subgenus is defined at present (quadrilamellate only).

The reproductive systems of three additional species assigned to subgenus *Holospira s.s.* have been published (Pilsbry, 1903; Gilbertson, 1989b). They are *H. (H.) sherbrookei* Gilbertson, 1989 from Arizona, *H. (H.) goldfussi* (Menke, 1847) from Texas and *H. (H.) nelsoni* Pilsbry, 1903 from Coahilla, Mexico. They exhibit arrangements of the reproductive system that are significantly different from *H. (H.) milleri* and from each other. Hence, it is apparent that *Holospira s.s.* is polyphyletic and in need of revision.

CONCLUDING REMARKS

Studies of the reproductive system indicate a greater than anticipated number of *Holospira* lineages from the northwestern corner of its range. Additional field work, especially in Mexico, is necessary for continued systematic evaluation of the genus. Examination of the soft anatomies of living populations is essential for an adequate understanding of their phylogeny. Eventually, the taxonomy of the entire genus should be revised to include anatomical data.

ACKNOWLEDGMENTS

I sincerely thank Edna Naranjo-Garcia, James E. Hoffman and Walter B. Miller for accompanying me on collecting expeditions including one to Sonora at which time we returned to sites of *Holospira* populations discovered many years earlier by Dr. Miller. These populations represent the Sonoran species whose anatomies are described herein. I also thank M. Andria Garback at the Philadelphia Academy of Sciences and Paul R. Greenhall at the National Museum of Natural History; Smithsonian Institution for the loan of type material of Sonoran *Holospira* spp. and Dwayne L. Moses for assistance with the illustrations. Dr. Miller and three anonymous reviewers offered many helpful suggestions. In addition, I thank the Professional Development Institute of Orange Coast College for awarding me partial release time from teaching duties for the preparation of this manuscript.

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APPENDIX 1.

Measurements (mm) of *Holospira* reproductive anatomies figured herein.

Species	Penis	Penial Retr. Muscle	Epi-phall.	Sperma-thecal Duct	Sperma-thecal Divert.	Sperma-theca	Free Ovid.
H.. danielsi	3.0	2.5	11.0	12.6	6.0	2.4	3.8
H. dentaxis alamellata	0.6	3.3	5.5	13.4	-	1.2	4.8
H. ferrissi	2.7	1.7	11.0	8.2	4.0	1.8	2.3
H. milleri	0.6	1.9	0.3	10.9	-	1.5	4.1
H. minima	2.0	3.0	8.2	12.1	-	1.6	3.8
H. remondi laevior	1.5	2.0	7.4	16.8	-	1.3	3.7
H. tantalus campestris	3.9	5.0	19.0	15.3	7.3	3.6	6.3

APPENDIX 2.

Measurements (mm) of *Holospira* shells figured herein.

Species	Height	Width
H. danielsi	11.7	3.9
H. dentaxis alamellata	11.7	4.0
H. ferrissi	8.1	3.4
H. milleri	13.1	3.7
H. minima	14.5	4.5
H. remondi laevior	14.5	4.7
H. tantalus campestris	10.0	3.8

APPENDIX 3.

Revised taxonomy of the genus *Holospira* from Arizona, Sonora and Sinaloa (*indicates those species for which the reproductive system has been described).

- Subgenus *Holospira*
  - *H. cyclostoma*
  - *H. milleri**
  - *H. sherbrookei**
- Subgenus *Allocoryphe*
  - *H. minima**
- Subgenus *Sonoraloa* subg. *nov.*
  - *H. remondi**
  - *H. dentaxis**
  - *H. mazatlanica*
- Subgenus *Eudistemma*
  - *H. arizonensis**
  - *H. chiricahuana**
  - *H. danielsi**
  - *H. ferrissi**
  - *H. millistriata*
  - *H. tantalus**
  - *H. whetstonensis*
- *Incertae sedis*
  - *H. kinonis*

Life History of the Endangered Fine-Rayed Pigtoe *Fusconaia cuneolus* (Bivalvia: Unionidae) in the Clinch River, Virginia

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Abstract. The reproductive cycle, fish hosts, and selected population statistics of the endangered fine-rayed pigtoe *Fusconaia cuneolus* (Lea, 1840) were investigated during 1986-1987 in the Clinch River, Virginia. Examination of gravid females and drift samples indicated that the summer brooder is gravid from mid-May to late July and releases most glochidia in mid-June. Diel samples of stream drift contained a peak of glochidia in early morning. Of 1619 collected and examined fishes of 39 species for glochidial attachment, infestation by amblemine glochidia was highest on cyprinids (27 - 46%). Six species were identified as likely hosts for glochidia of the fine-rayed pigtoe. Induced infestations of fishes with glochidia in the laboratory confirmed eight host species: fathead minnow *(Pimephales promelas)*; river chub *(Nocomis micropogon)*; stoneroller *(Campostoma anomalum)*; telescope shiner *(Notropis telescopus)*; Tennessee shiner *(N. leuciodus)*; white shiner *(Luxilus albeolus)*; whitetail shiner *(Cyprinella galactura)*; mottled sculpin *(Cottus bairdi)*.

Age class and growth rate characteristics, determined by sectioning of valves collected in muskrat middens, were similar between two demes in the river. The fine-rayed pigtoe reaches a maximum length of about 90 mm and age of 35 yr. Annual growth averaged 5 mm/yr through age 10 and decreased to about 2 mm/yr thereafter until senescence. Specimens less than age 10 were uncommon, and no individuals under age 6 were collected. Cohort structure of live specimens and collections of valves indicated that the fine-rayed pigtoe population is declining in the Clinch River, Virginia.

The upper Tennessee River watershed in southwestern Virginia harbors a diverse assemblage of freshwater mussels (Unionidae) that seems to be in significant decline. Of the roughly 45 reported species from this region, 13 are listed as endangered by the federal government and another 20 are proposed for protection by Virginia (Neves, 1991). Declines in abundance and diversity of mussels are due largely to anthropogenic activities (Bates and Dennis, 1978; Ahlstedt, 1984). However, a consortium of state and federal agencies now are involved actively in the protection and recovery of biodiversity in these rivers.

The fine-rayed pigtoe pearly mussel *Fusconaia cuneolus* (Lea, 1840) was listed as endangered on 14 June 1976 (Federal Register 41:24062-24067). Historically this species was widespread in tributaries of the Tennessee River in Virginia, Tennessee, and Alabama, but now is restricted to reaches of seven rivers in the upper and lower Tennessee River system. The largest population occurs upstream of Norris Reservoir in the Clinch River, Virginia and Tennessee (Fig. 1). Ortmann (1921) noted that this species was a short-term brooder (tachytictic), breeding from May to July, and that all four gills served as marsupia for its glochidia, which are subelliptical in shape and of similar length and height (0.16 mm). Other aspects of its biology and life history were unknown. The objectives of this study, therefore, were to describe the chronology of the reproductive cycle, identify fish hosts, and determine the demographics of two demes of the fine-rayed pigtoe in the Clinch River, Virginia.

STUDY SITE

The principal study site was at Slant, Clinch River Mile (CRM) 223.3 in Scott County, Virginia (Fig. 2). From an

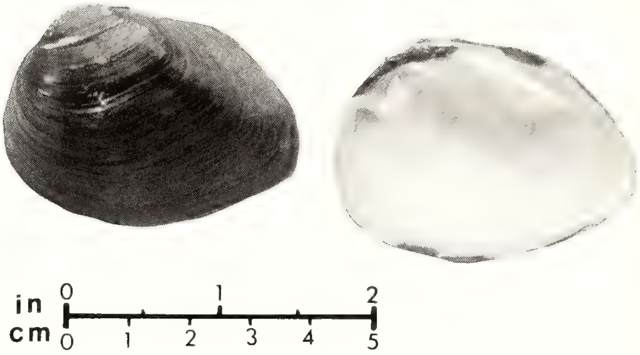

Fig. 1. Specimen of *Fusconaia cuneolus* from the Clinch River, Virginia.

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[2] The Unit is jointly supported by the United States Fish and Wildlife Service, the Virginia Department of Game and Inland Fisheries, the Wildlife Management Institute, and Virginia Polytechnic Institute and State University

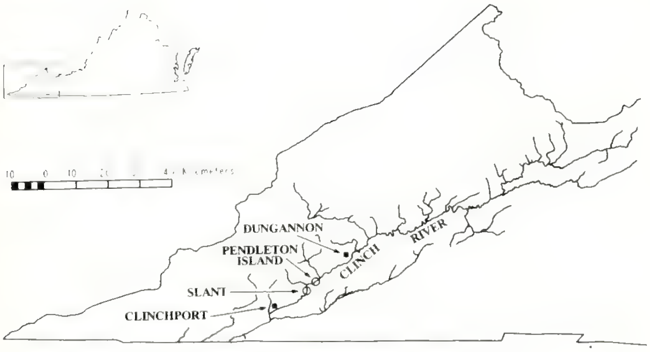

Fig. 2. Location of study sites on the Clinch River, Virginia.

assessment of muskrat predation on endangered mussels in the Clinch River, Neves and Odom (1989) recorded 32 mussel species and a large population of the fine-rayed pigtoe at this site. The river reach with *Fusconaia cuneolus* was approximately 325 m long and 50 m wide, with substrata of coarse gravel, cobbles, and bedrock. One additional site at Pendleton Island (CRM 226.3), a preserve of The Nature Conservancy, provided gravid females for glochidia and fresh-dead valves for demographic analysis.

MATERIALS AND METHODS

FIELD STUDIES

During the summers of 1986 and 1987, we monitored the incidence of gravid females at the study sites. Specimens of *Fusconaia cuneolus* were opened carefully with modified o-ring expanders to examine gills. Because this species is not sexually dimorphic in shell characters, gender could be determined only during the period of gravidity. Gravid females were identified by intensely pink and enlarged marsupial gills (Ortmann, 1921). Observations of weekly changes in coloration of female gills (marsupia) in 1986 prompted a more detailed examination in 1987. At Slant, examined females were placed under hardware mesh cloth in 1986 to prevent depredation by muskrats. In 1987, these stockpiled females were marked with 5 mm x 3 mm numbered disc tags (Floy Tag Co., Seattle, Washington[3]) to allow weekly monitoring of individuals. We recorded date, color of gills, and percent gravid females. Mid-day water temperatures were recorded at Slant with a max-min thermometer. Fecundity was computed from the number of conglutinates in a sacrified female (70 mm length) and the mean number of embryos per conglutinate.

Because the glochidia of *Fusconaia cuneolus* were similar in appearance to three other species of the subfamily Ambleminae at the study site, we collected and statistically compared glochidia from each of five specimens of these other amblemine mussel species: long-solid *F. subrotunda* (Lea, 1831); shiny pigtoe *F. cor* (Conrad, 1834); Tennessee clubshell *Pleurobema oviforme* (Conrad, 1834). Glochidia of mussel species in the subfamily Ambleminae are distinguishable by their characteristic size and shape (Neves and Widlak, 1988). Sample sizes were 50 glochidia for the *Fusconaia* spp. and 42 glochidia for *P. oviforme*. Expelled glochidia from gravid specimens were measured in length, width, and hinge lengths (Table 1). A Kruskal-Wallis test was used to determine whether valve dimensions differed among species. An LSD procedure with ranks identified those dimensions that were significantly different.

To determine the period of release of glochidia, we sampled stream drift weekly with three square-framed drift nets (0.045 m^2) of 130 um mesh nylon netting with removable cod-ends. Drift nets were staked into the river bottom downstream of a mussel bed on a line transect for roughly 1 hr between 1000 and 1500 hr on each sampling date. Drift samples were collected from 16 June to 13 Aug 1986, and 29 May to 30 July 1987. Samples were preserved in 10% formalin buffered with sodium borate to prevent dissolution of glochidial valves. In the laboratory, rose bengal was added to samples to facilitate recognition of glochidia. A 0.5 mm mesh sieve was used to remove large particulate matter, and finer debris and glochidia were collected in a 130 um mesh sieve. The latter was examined in a gridded petri dish with a dissecting microscope (25-40X) and glochidia were removed and counted. Densities of glochidia were computed from measurements of water depth and water velocity at the net opening and from counts of glochidia per sample.

The diel periodicity of glochidial release of *Fusconaia cuneolus* was determined at Slant on 16-17 June 1987, the recorded time of peak release in 1986. Every 4 hr during a 24 hr period, we positioned one drift net in the stream where the greatest densities of glochidia were collected in 1986. Numbers of glochidia were tabulated for each of the six time periods to compare densities in a 24 hr daily cycle.

The fish fauna at Slant was sampled for roughly 2 hr weekly in a 100 m section of the river with a backpack electroshocker and dip nets. Stunned fishes were collected, sorted and preserved in 10% buffered formalin. In the laboratory, opercular flaps were removed to examine gills with a dissecting microscope (20-40X). No amblemine glochidia were observed externally on the fishes. We tabulated frequency of occurrence and number of glochidia per fish. Fish species with encysted amblemine glochidia were considered possible hosts for the fine-rayed pigtoe.

LABORATORY INFESTATIONS

We confirmed fish hosts of the fine-rayed pigtoe in the laboratory by induced infestations of putative fish hosts with glochidia. Dechlorinated tap water, oxygenated by Venturi-type diffuser aerators, was recirculated through a central

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[3] Reference to trade names does not imply government endorsement of commercial products.

Table. 1. Mean dimensions (mm) ± SD and morphometric comparisons of glochidia of selected amblemine species from the Clinch River, Virginia.

Glochidial dimension	*Pleurobema oviforme*	*Fusconaia cuneolus*	*F. cor*	*F. subrotunda*
Length	0.185 ± 0.007	0.181 ± 0.008	0.181 ± 0.006	0.181 ± 0.009
Width	0.193 ± 0.004	0.193 ± 0.005	0.146 ± 0.006	0.150 ± 0.028
Hinge length	0.150 ± 0.005	0.165 ± .009	0.122 ± 0.005	0.118 ± 0.005

Underscore indicates no difference between species ($p \geq 0.05$).

gravel biofilter and 96 L rectangular tanks. Fishes for induced infestations were collected from river reaches in Virginia, where mussels were absent or rare, to eliminate the possibility of acquired immunity from prior exposure to glochidia (Neves *et al.*, 1985). Target fish species were electroshocked, scooped with a bucket, and transported in coolers containing aerated river water and 2% salt solution. Ice packs were added when necessary to maintain water temperatures (20°-26°C) comparable to those in laboratory holding tanks.

Prior to infestations, collected fishes were acclimated for approximately five days. A 4% benzocaine solution was used to anesthetize fishes and facilitate the identification of cyprinids. Fishes were sorted by species into separate tanks, and the tops of standpipes were covered with 5 mm mesh screen to prevent escape.

Mature glochidia were obtained from gravid females collected at Pendleton Island and Slant, Virginia. Mussels were transported to the laboratory and induced to abort conglutinates by placing them in individual 400 ml beakers without substratum. Beakers were set in a Living Stream (Frigid Units, Inc., Toledo, OH) at a mean temperature of 22°C until glochidia were expelled. If females failed to release glochidia after five days, the beakers were removed from the stream and held at room temperature (23°C). The increased temperature and static water were usually effective in promoting expulsion of glochidia. Conglutinates were retrieved with a large-bore pipette, and glochidia were extricated from the conglutinate by repeated agitation in a finger bowl. Infestations were performed with three containers to hold, anesthetize, and recover infested fishes. Procedures for infestation, examination of fishes, and recovery of juveniles were performed according to Zale and Neves (1982). Juveniles were identified by their yellowish color, thickened ventral margins, and movement of the protruding foot. A sample of juveniles was relaxed in propylene phenoxitol, preserved in 10% buffered formalin, and later photographed. A fish species was considered a host of the fine-rayed pigtoe if encystment and metamorphosis to the juvenile stage occurred. Most laboratory tests that confirmed host fish species in 1986 were repeated in 1987.

AGE AND GROWTH

Valves of the fine-rayed pigtoe, collected at Pendleton Island and Slant, were measured and aged by thin-sectioning with a Buehler Isomet low-speed diamond-tipped saw (Buehler Ltd., Evanston, Illinois). Five to ten valves per length group (10 mm intervals) from each site were thin-sectioned (Neves and Moyer, 1988). Age of each specimen was determined by counting internal growth lines on thin-sections using a compound microscope (50X). The point where the annulus reached the valve margin was marked with a black felt-tipped pen. The marked thin-sections then were held facing the cross-section from which the cut was produced. Internal growth lines were compared with external growth lines, and false annuli were identified (Neves and Moyer, 1988). Because specimens younger than age nine were rare, we obtained back-measured lengths of younger age groups. On five specimens from each site, external annuli on their cross-sections were marked. By overlaying this valve section onto the matching uncut valve, we measured lengths of the growth lines at previous ages. For these back-measured lengths, we used valves with minimal erosion and easily distinguished annuli.

Total lengths by age were obtained from thin sections and fitted to a modified version of the von Bertalanffy growth equation (Gallucci and Quinn, 1979):

$$L_t = (w/k)\ (1-e^{-k\ (t-to)})$$

where t is a given age in years, t_o is the theoretical time when length is zero, k is a growth constant,and w describes growth rate near t_o. The parameter w is the product of K and $L\infty$ and replaces $L\infty$ in the original von Bertalanffy equation. Gallucci and Quinn (1979) concluded that this new parameter (w), because of its statistical robustness, allows comparison of growth rates among populations. Non-linear procedures were applied to derive estimates of w, k, and t_o. Based on these values, estimates of L_t were computed (SAS Institute, 1982). Confidence intervals of parameter estimates were compared for overlap to determine differences in growth of *Fusconaia cuneolus* between sites. The equation of predicted lengths at each age, derived from thin-sectioned valves, was used to predict ages from total lengths of unaged specimens.

We obtained lengths from valves of *Fusconaia cuneolus* collected in muskrat middens at Slant from 1980 to 1986. Ages of 353 mussels in this collection were computed by age-length relationships, and the age-class distribution of the deme at this site was determined. Lengths of 43 live specimens, randomly collected at Slant in 1987, also were converted to ages to determine age class structure. The two age distributions were compared with the G-test (R X C test of independence) to determine whether collection method (human vs muskrat) influenced interpretation of sampling results.

Nomenclature for mussels is according to Turgeon *et al.* (1988). Binomials for fishes follow Robins *et al.* (1991).

RESULTS

REPRODUCTIVE CYCLE

Gravid females of the fine-rayed pigtoe were collected first on 16 June 1986. Four of eight specimens were gravid. Between 16 July and 6 Aug 1986, percent gravidity was high (50-100%), but sample size on each date was small (N = 4). However, a random sample of 33 fine-rayed pigtoes collected at Pendleton Island on 25 July also indicated that many females (61%) were gravid during this time. One female was gravid at Slant on 6 Aug. No gravid specimens were collected thereafter.

In 1987, two gravid females were collected on 10 June (Fig. 3). Most of the stockpiled females at Slant were collected again on 18 June 1987. Gravid specimens were collected as late as 6 Aug 1987 at Pendleton Island, which corroborated our observations in 1986. Females began incubating eggs in early to mid-May, as judged by the additional collection and examination of females in 1988. Females were not gravid at Pendleton Island (N = 21) or Slant (N = 27) on 3 May, but by 23 May, one of 12 gravid females examined at Slant and nine of 20 at Pendleton Island were gravid. Mid-day water temperatures at Slant increased from 16° to 21°C during this time period.

Table 2. Water temperatures and densities of glochidia of the fine-rayed pigtoe in weekly drift samples from the Clinch River at Slant, Virginia, 1986 and 1987.

Sample date	Temperature range (°C)	Weekly median temperatures (°C)	Glochidial densities (no/100m³)
1986			
6/16	—	25.4	43.0
6/25	21.4-27.4	24.4	1.9
7/01	22.4-27.9	25.1	6.6
7/09	23.4-27.9	25.6	27.0
7/16	24.4-28.4	26.4	39.7
7/25	25.4-29.9	27.6	8.9
7/30	24.4-29.4	26.9	9.4
8/05	21.4-28.4	24.9	2.9
8/13	22.9-27.4	25.1	3.9
1987			
5/29	—	25.4	1.7
6/10	—	23.0	54.7
6/18	22.9-24.9	23.0	126.6
6/24	23.4-25.1	24.0	38.3
7/01	23.0-25.6	23.5	20.8
7/08	22.0-24.3	23.0	60.3
7/16	21.6-24.2	23.5	3.9
7/20	21.9-24.0	23.3	7.9
7/30	25.0-27.4	26.0	0.8
8/05	26.2-28.0	26.8	—

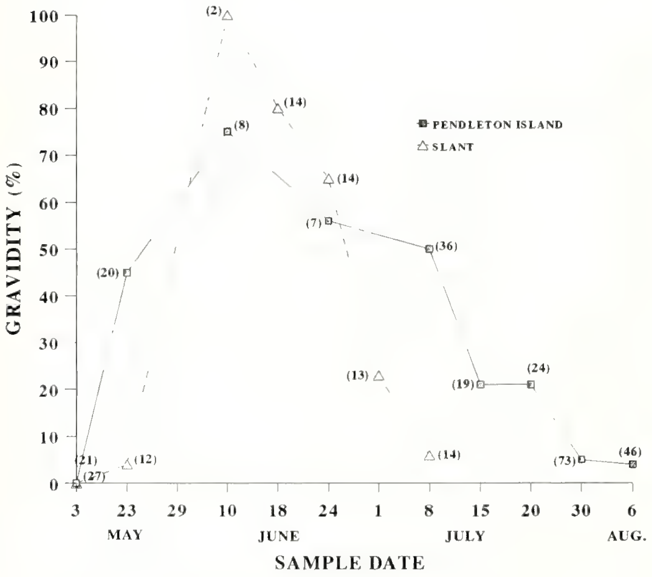

Fig. 3. Frequency of gravid females in the Clinch River, Virginia, during summers, 1987 and 1988 combined (sample sizes in parentheses).

The marsupia of all gravid females collected on 10 June and 4 July contained peach-colored conglutinates. By frequent examination of females at Slant and those brought to the laboratory, we noted a change in marsupial color with maturity - from pink to orange to light peach. In the laboratory, females with light peach marsupia consistently released mature glochidia, held together in a loose gelatinous matrix. Females released mature glochidia within seven to 14 days after the pink color was observed, at water temperatures between 20° and 24°C. Development from embryo to glochidium required roughly 2 wk within this temperature range.

Mature glochidia were light orange to peach in color and free of vitelline membranes. Unfertilized eggs, embryos, and immature glochidia were distinctively pink, but unfertilized eggs lacked vitelline membranes. When aborted, immature glochidia were enclosed in tightly organized, pink conglutinates. Marsupia of females, immediately following release of glochidia, exhibited a bubbly appearance and were less turgid than the gills of gravid females.

Table 3. Incidence of glochidial infestations on cyprinid species from the Clinch River, Virginia, 17 June to 30 July, 1987.

Species	No. examined	No. infested		% infested	
		Ambleminae	Other	Ambleminae	Other
Notropis amblops (Rafinesque, 1820)	265	1	26	0.4	9.8
N. volucellus (Cope, 1865)	199	54	44	27.1	22.1
Campostoma anomalum (Rafinesque, 1820)	88	7	5	8.0	5.7
Luxilus chrysocephalus Rafinesque, 1820	59	4	8	6.8	13.6
N. sp.	48	22	12	45.8	25.0
N. ariommus (Cope, 1868)	46	1	2	2.2	4.3
Nocomis micropogon (Cope, 1865)	45	14	3	31.1	6.7
Erimystax dissimilis (Kirtland, 1840)	41	0	0	0.0	0.0
Cyprinella galactura (Cope, 1868)	33	13	8	39.4	24.2
Notropis telescopus (Cope, 1868)	31	2	1	6.7	3.2
L. coccogenis (Cope, 1868)	30	2	1	6.7	3.3
N. leuciodus (Cope, 1868)	20	6	2	30.0	10.0
E. insignis (Hubbs and Crowe, 1956)	18	0	0	0.0	0.0
C. spiloptera (Cope, 1868)	13	4	2	30.8	15.4
Pimephales notatus (Rafinesque, 1820)	8	1	0	12.5	0.0
Phenacobius uranops Cope, 1867	8	0	0	0.0	0.0
N. photogenis (Cope, 1865)	7	0	0	0.0	0.0
C. whipplei Girard, 1856	4	0	2	0.0	5.0
N. rubellus (Agassiz, 1850)	2	0	0	0.0	0.0
Total	965	131	116		

For host fish experiments, only females with peach-colored marsupia were transported to the laboratory. The 41 gravid females held in the laboratory during 1987 released glochidia from 14 June to 11 Aug at water temperatures between 20° and 24°C. Thirty-three females released conglutinates with nearly 99% mature, viable glochidia. Eight females released conglutinates with 3 to 5% unfertilized eggs. Immature glochidia were released by only one female on 19 July.

Conglutinates were subcylindrical in shape and approximately 6 mm long and 1.5 mm wide with two layers of tightly aggregated glochidia about 0.8 mm deep. One conglutinate from each of five females contained a mean of 236 ± 38.1 embryos or glochidia. Fecundity was about 113,000 embryos for the sacrificed female.

Hinge lengths differed among each of the four amblemine species (Table 1; $p = 0.0001$, $n = 42\text{-}50$ glochidia per species). Glochidia of *Fusconaia cuneolus* were greater in width than those of *F. cor* and *F. subrotunda*, but were not different from those of *Pleurobema oviforme.* Total lengths of glochidia of all species did not differ. The glochidia of the fine-rayed pigtoe most closely resembled those of *P. oviforme*, but were visually distinguished by a longer hinge length and more rotund appearance.

We observed two peaks in the presence of glochidia in 1986 and 1987 (Table 2). In 1986, peak densities of glochidia occurred in mid-June (43.0/100 m^3) and mid-July (39.7/100 m^3). A similar trend in densities was observed in 1987, although the second peak occurred one week earlier than in 1986. Multiple linear regression analyses indicated that densities of glochidia were not correlated with date of sample, weekly median temperature prior to sample date, or water velocity at the drift net.

From 16 to 17 July 1987, we collected glochidia of *Fusconaia cuneolus* in stream drift throughout the 24 hr period, at water temperatures ranging from 21.2° to 23.0°C. Densities of glochidia were lowest at 2300 and 0300 hr (1/100 m^3) and peaked at 0700 hr (118/100 m^3). Water velocity at the drift net was constant at 0.4 m/sec for the period.

FISH HOSTS

From 17 June to 30 July 1987, we collected and examined 1,150 fishes representing 39 species at Slant for attached glochidia. Thirteen fish species, all cyprinids, were infested with glochidia of the Ambleminae (Table 3). The highest prevalence of infestation on cyprinids occurred on 17 June (17%) and 8 July (25%) 1987 (Table 4), dates corresponding to the highest densities of glochidia of *Fusconaia cuneolus* in stream drift. Minnow species with the highest incidence of infestation were the sawfin shiner *Notropis* sp. (45.8%), whitetail shiner *Cyprinella galactura* (Cope, 1868) (39.4%), river chub *Nocomis micropogon* (Cope, 1865) (31.1%), spotfin shiner *C. spiloptera* (Cope, 1868) (30.8%), Tennessee shiner *Notropis leuciodus* (Cope, 1868) (30%) and mimic shiner *N. volucellus* (Cope, 1865) (27.1%). These fish species were identified as the most probable hosts for the fine-rayed pigtoe.

On various sample dates in 1987, glochidia identified as *Fusconaia cuneolus* were found encysted in the gills of four species of cyprinids; river chub, whitetail shiner, stoneroller,

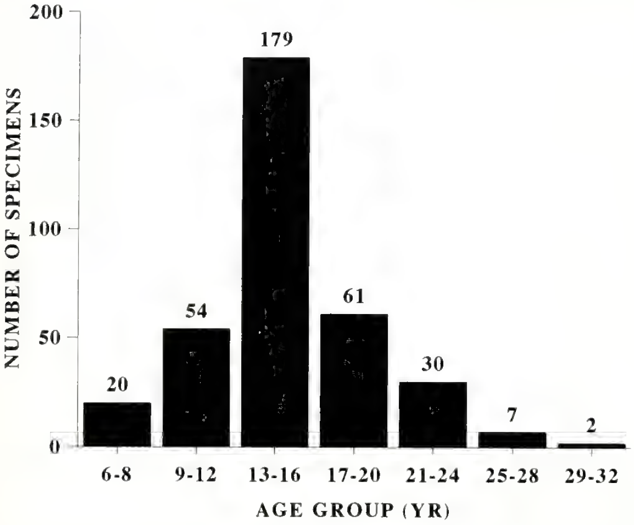

Fig. 4. Age class structure of fine-rayed pigtoes collected in muskrat middens from the Clinch River at Slant, Virginia, 1984-85.

and spotfin shiner. Newly metamorphosed juveniles of the fine-rayed pigtoe were observed on the gills of river chubs on all weekly sample dates between 8 and 30 July 1987. Gills of spotfin shiners also harbored newly metamorphosed juveniles of *F. cuneolus* on 21 and 30 July. These young juveniles, easily removed from cysts with a dissecting needle, exhibited the typical yellowish color and thickened ventral margins. The degree of infestation of the fine-rayed pigtoe on individual fish ranged from one to 26 glochidia. Numbers of glochidia per fish were highest for the river chub (1-26 glochidia/fish); however, most infested fishes carried one to five glochidia per individual.

In laboratory exposures, glochidia of *Fusconaia cuneolus* were sloughed from the gills of eight of the 16 fish species tested (Table 5). Seven infested non-cyprinid species were not considered hosts because they sloughed glochidia usually within one to five days. However, the fantail darter *Etheostoma flabellare* Rafinesque, 1819 retained glochidia for nine days, and the goldfish *Carassius auratus* (Linnaeus, 1758), for six days. The goldfish was the only examined minnow that did not serve as a host.

Seven species of cyprinids and the mottled sculpin *Cottus bairdi* Girard, 1850 were confirmed as fish hosts (Table 6). The periods of metamorphosis ranged from 10 to 19 days at mean water temperatures between 22.5° and 25.0°C. At mean water temperatures of about 23°C, most juveniles were collected 15 to 16 days post-infestation. Peak numbers of juveniles were collected from river chubs on day 11 at 24°C and from mottled sculpins on day 13 at 25°C.

AGE AND GROWTH

The pattern of growth in shell length of the fine-rayed pigtoe was asymptotic. Mean annual growth in length averaged 5.0 mm/yr before age six, 3.7 mm/yr between ages six and 16, and 2.1 mm/yr between ages 16 to 21 (Table 7). Thereafter, growth slowed to roughly 1 mm/yr. Growth equations describing increases in length were as follows:

$$L_t = (10.4/0.13)\ (1 - e^{-0.13\ (t - 0.05)}) \text{ at Pendleton Island;}$$
$$L_t = (\ 7.3/0.08)\ (1 - e^{-0.08\ (t - 0.031)}) \text{ at Slant.}$$

Except for more rapid growth of juveniles up to age five at Pendleton Island, all subsequent growth increments were similar between the two sites.

The ages of live specimens of fine-rayed pigtoes at both sites ranged from six to 32 years; individuals 17 to 20 years old were the dominant age groups (Table 8). The most common specimens found in muskrat middens (Fig. 4) were 13 to 16 years old. Younger specimens (< age 10) were more common in muskrat middens than in the sample of live specimens collected by snorkeling and handpicking. Similarly,

Table 4. Dates of infestation of amblemine glochidia on cyprinids from the Clinch River at Slant, Virginia, summer 1987.

Sample date	No. examined	No. infested	% infested
17 June	102	17	17
25 June	71	7	10
8 July	118	29	25
16 July	184	27	15
21 July	305	34	11
30 July	179	18	10
Total	959	122	

Table 5. Fish species that did not serve as hosts for the glochidia of the fine-rayed pigtoe in laboratory experiments.

Infested species	No. infested	Temperature range (°C)	Last day of observed attachment
Centrarchidae			
Lepomis macrochirus Rafinesque, 1819	4	21.0-24.0	5
L. auratus (Linnaeus, 1758)	1	20.0-25.0	5
Ambloplites rupestris (Rafinesque, 1817)	5	24.0-26.0	2
Cyprinidae			
Carassius auratus (Linnaeus, 1758)	10	24.0-25.0	6
Ictaluridae			
Ictalurus punctatus Rafinesque, 1818)	6	24.0	1
Noturus insignis (Richardson, 1836)	4	24.0	1
Percidae			
Etheostoma flabellare Rafinesque, 1819	7	24.0-26.0	9
E. rufilineatum (Cope, 1870)	10	24.0-26.0	4

a greater percentage of old individuals were included in the collection of live mussels ($X^2 = 76.6$, 2 df, $p = 0.0001$, $n = 580$). Young specimens were rarely found at either site, but several specimens (age six) were collected in muskrat middens at Slant.

DISCUSSION

Our conclusion that the fine-rayed pigtoe is a short-term brooder and gravid from mid-May to early August in the Clinch River corroborates Ortmann's (1921) records of gravidity (16 May - 13 July) for this species in the upper Tennessee River drainage and is in general agreement with the chronology of reproduction by other short-term brooders (Yokley, 1972; Yeager and Neves, 1986). The fine-rayed pigtoe appears to spawn and incubate eggs when water temperatures reach 16°C. Seasonal change in temperature is often noted as an important environmental cue for spawning of mussels (Coker *et al.*, 1921; Matteson, 1948; Yokley, 1972; Smith, 1976). The above-normal air temperatures and below-normal precipitation during summer 1986 (Virginia Agricultural Statistics Service, 1987) could account for differences we observed in the reproductive cycle between 1986 and 1987.

We were able to follow the development of embryos by monitoring color changes of the marsupia (conglutinates within). Yeager and Neves (1986) noted color changes of the marsupia of the rough rabbitsfoot *Quadrula cylindrica strigillata* (Wright, 1898), and this trait seems useful for categorizing the maturity of glochidia. As judged by observed color changes, the development of fertilized eggs to glochidia requires approximately 2 wk for fine-rayed pigtoes. Because early embryos occur in female marsupia shortly after spawning (Coker *et al.*, 1921; Zale and Neves, 1982), we postulate that *Fusconaia cuneolus* spawns in early May. Histological studies of other amblemine species support this conclusion (Matteson, 1948; Yokley, 1972; Yeager and Neves, 1986).

Glochidia of the fine-rayed pigtoe exhibited considerable host specificity, primarily to fishes of the Cyprinidae. The relationship between short-term brooders and cyprinids appears to apply throughout the upper Tennessee River drainage (Yeager and Neves, 1986; Neves and Widlak, 1988). As judged by the prevalence of natural infestations on the river chub, whitetail shiner, and Tennessee shiner, we believe that these fish species are primary hosts for the fine-rayed pigtoe in the Clinch River. Further, these fish species are widespread and common in the Clinch River and other tributaries to the upper and lower Tennessee River. The use of multiple hosts by a freshwater mussel in a dynamic, lotic environment has obvious survival value (Trdan and Hoeh, 1982; Kat, 1984). Because the genera *Notropis* and *Cyprinella* tend to dominate the cyprinid assemblages in most southeastern rivers, confirmed hosts and congeneric species in rivers with the fine-rayed pigtoe probably serve as hosts. Subsequent research on host fishes with other endangered populations of *Fusconaia cuneolus* should focus on the cyprinid assemblage in their respective rivers.

We recorded only one to five glochidia on most naturally infested fishes, and this low level of infestation is seemingly typical of riverine mussel species (Neves and Widlak, 1988). Early studies concluded that fish species with few encysted glochidia were probably incidental hosts (Surber, 1912; Howard and Anson, 1922; Tedla and Fernando, 1969), but low degrees of infestation seem to be the rule rather than the exception. River chubs and *Notropis* spp. commonly feed on drifting insects and could become infested by feeding on released conglutinates in the water column and, therefore, experience a higher degree of infestation (Neves and Widlak, 1988). Conversely, the stoneroller is a grazing minnow that feeds principally by scraping aufwuchs from rocks and other substrata. Although both feeding groups can become infested (Table 3), our data suggest that cyprinids feeding visually in the water column are the primary fish hosts for the fine-rayed

Table 6. Fish species that served as hosts for the glochidia of the fine-rayed pigtoe in laboratory experiments.

Infested species	No. infested	Period of metarmorphosis	Peak day of excystment	Temperature range (°C)	No. juveniles recovered
Cyprinidae					
Pimephales notatus	10	12-16	15	21.0-26.0	76
Nocomis micropogon	2[1]	11-19	11	22.0-25.5	50
Campostoma anomalum	3	12-16	15	21.0-26.0	537
Notropis telecopus	8	10-16	15	22.0-23.5	101
N. leuciodus	9[2]	13-14	—	22.0-23.0	2
Luxilus albeolus	6	10-18	16	21.0-26.0	424
Cyprinella galactura	10	12-16	16	22.0-23.5	760
Cottidae					
Cottus bairdi	7	12-14	13	24.0-26.0	84

[1] Experiment performed in 1986

[2] All died from disease prior to completion of experiment

Table 7. Sample size and observed and predicted lengths of the fine-rayed pigtoe in the Clinch River at Slant, Virginia.

Age	N	Observed length mean ± 1 s.d.	Predicted length
1	10	8.6 ± 1.7	5.0
2	10	12.9 ± 1.9	11.6
3	9	18.7 ± 4.2	24.8
4	10	24.0 ± 4.5	23.3
5	10	28.3 ± 3.8	28.5
6	11	32.7 ± 4.4	33.2
7	11	37.6 ± 5.9	37.7
8	10	37.8 ± 2.6	41.8
9	2	43.9 ± 1.9	45.5
10	8	46.1 ± 7.6	49.0
11	2	55.5 ± 8.7	52.5
12	8	56.1 ± 5.0	55.2
13	6	57.4 ± 7.8	58.0
15	5	65.3 ± 5.0	62.8
16	3	68.6 ± 6.8	65.0
17	1	71.7 —	67.0
18	1	74.8 —	68.8
20	2	73.5 ± 3.8	72.1
23	1	65.9 —	76.1
25	1	77.0 —	78.2
27	1	83.6 —	80.1
30	1	80.2 —	82.4

pigtoe.

The mottled sculpin was the only non-cyprinid that served as host for the fine-rayed pigtoe. This species was not collected at Slant. Although sculpins are ubiquitous in the Tennessee River system, the mottled sculpin is rare whereas the banded sculpin is common throughout the upper Clinch River. Neves *et al.* (1985) determined that congeneric, allopatric species can serve as fish hosts; therefore, the suitability of *Cottus* spp. as hosts is likely. Weaver (1981) documented that the banded sculpin served as host for the Tennessee clubshell in laboratory trials, but she observed no natural infestations on it in Big Moccasin Creek, Virginia. Therefore, sculpins seem to be suitable but not primary hosts for short-term brooders in southwest Virginia.

Because the fine-rayed pigtoe is a slow-growing species with frequent erosion of umbos, examination of thin-sections under magnification was essential for accurate aging. On average, 1 to 1.5 hr was required to prepare each valve, and an additional 12 hr for drying the epoxy. Recognition of false annuli was apparent on thin sections (Neves and Moyer, 1988). The growth pattern for the fine-rayed pigtoe at Pendleton Island was very similar to that reported by Moyer (1984) for a downstream deme of this species. Asymptotic lengths and estimates of K were comparable, but values of t_0 were different. This discrepancy is most likely explained by estimates of length at age one. Eroded umbos usually obliterate the first annulus, and estimates are often best guesses. Mean lengths of some cohorts were underestimated by the growth equation, but they concurred with empirical data when sample sizes were greater than five mussels. Because we were unable to obtain suitable numbers of both old and young mussels for aging, predicted lengths at these ages could be more accurate than observed values.

Theoretical maximum lengths ($L\infty$) and estimated values of K were different between demes at Slant and Pendleton Island, but these parameters are unsuitable for comparison among populations (Gallucci and Quinn, 1979; Haukioja and Hakala, 1979). However the parameter w, which is suitable for comparison (Gallucci and Quinn, 1979), was significantly different between sites. Fine-rayed pigtoes grew faster at Pendleton Island than at Slant. We attribute this difference to the shallower water depths and greater water velocities at Pendleton Island that probably increased oxygen levels and the availability of food particles per unit time for filter-feeders.

The age range (6 to 32) of fine-rayed pigtoes and the dominance of few, older cohorts in this reach of the Clinch River were unexpected. The population of *Fusconaia cuneolus* in the Clinch River is considered to be the largest and healthiest (U.S. Fish and Wildlife Service, 1984). Although freshwater mussel populations are dominated commonly by older cohorts, sampling techniques often contribute to that age (size) bias (Chamberlain, 1931; Coon *et al.*, 1977). Our sampling results suggested that because of the predation and apparent selectivity of fine-rayed pigtoes over other species by muskrats at Slant (Neves and Odom, 1989), determination of age-class structure from specimens in muskrat middens provided a reasonable assessment of population demographics. The lack of fine-rayed pigtoes < age 10 in a large sample (N = 264) from muskrat middens indicated that recruitment is poor. Similarly, the reduction in population size from muskrat predation has been large (Neves and Odom, 1989). As computed from the age-length relationship for the fine-rayed pigtoe, ages 11 to 14 (56-65 mm) were consumed by muskrats with greatest frequency. The removal of members of these age groups and the rare occurrence of mussels < age 10 has reduced the reproductive potential and likely will jeopardize the continued abundance of this species

Table 8. Comparison of age class structure of live specimens and fresh-dead valves (muskrat middens) of the fine-rayed pigtoe from the Clinch River, Virginia[1].

	Midden Shells		Live Specimens	
Age Class	No.	Percent	No.	Percent
< 10	79	22.4	8	3.5
11-20	263	74.5	176	77.5
21-30	11	3.1	43	19.0
Total	353	100	227	100

[1] RXC test of independence with the G-test with Williams correction (X^2 = 76.6, 2 df, p = 0.0001).

at study sites in the Clinch River. Recent sampling and monitoring of mussels at various sites on the Clinch River, Virginia suggest that the fine-rayed pigtoe and other mussel species are declining in abundance in most reaches of the Clinch River. A new cooperative effort by governmental agencies and conservation organizations is underway to identify and remedy the factors that are contributing to the loss of freshwater mussel populations in this river.

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Comparative feeding biology of *Acteocina canaliculata* (Say, 1826) and *Haminoea solitaria* (Say, 1822) (Opisthobranchia: Cephalaspidea)

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Abstract. The southern New England cephalaspidean *Acteocina canaliculata* (Say, 1826) feeds on bivalves, including *Gemma gemma* (Totten, 1834), and Foraminifera belonging to three suborders: Textulariina, Miliolina, and Rotaliina. The proportion of miliolid foraminiferans in the diet of *A. canaliculata* decreased with increasing snail size. Snails > 5.0 mm in shell length fed increasingly on bivalves, probably reflecting an inability of small snails to ingest large prey. The snails appear to locate prey with the aid of Hancock's organ and sensory patches (here reported for the first time) situated along the anterior edge of the cephalic shield and foot. Individual prey are grasped with the radula and pulled whole into the buccal cavity. Sediment particles appear to be removed passively by the jaws. *Haminoea solitaria* (Say, 1822) indiscriminately ingests sediment containing diatoms, unidentified algae, and detritus. Hancock's organ and sensory palps in *H. solitaria* probably do not aid in selection of specific food particles, but could be involved in location of areas where diatoms and algae are abundant.

Cephalaspidean opisthobranchs are common members of the shallow water marine benthos. Previous studies revealed that cephalaspids feed on a variety of food items, including bivalve and gastropod mollusks (Hurst, 1965; Berry, 1988; Berry and Thompson, 1990; Morton and Chiu, 1990), foraminiferans (Burn and Bell, 1974a, b; Shonman and Nybakken, 1978; Berry, 1988; Berry and Thompson, 1990), polychaete worms (Hurst, 1965; Rudman, 1972a, b; Yonow, 1989), and algae (Fretter, 1939; Rudman, 1972a). Few studies have dealt with the feeding habits of cephalaspids in detail. Two species, *Acteocina canaliculata* (Say, 1826) and *Haminoea solitaria* (Say, 1822), occur commonly along the New England coast (Abbott, 1974) and offer an opportunity to investigate and contrast the feeding biology of two genera in detail.

Acteocina canaliculata is a small (4-6 mm) opisthobranch found commonly in both oceanic and estuarine environments in bare or vegetated, sandy to muddy subtidal habitats (Franz, 1971; Gosliner, 1979; Mikkelsen and Mikkelsen, 1984). The only species of *Acteocina* studied previously with regard to feeding, *A. culcitella* (Gould, 1852), is a selective predator on foraminiferans (Shonman and Nybakken, 1978).

Haminoea solitaria, another small (10-12 mm) opisthobranch, occurs in environments similar to those of *Acteocina canaliculata*. Except for *H. brevis* (Quoy and Gaimard, 1833), which is reported to feed on bivalve mollusks (MacPherson and Gabriel, 1962), members of the genus *Haminoea* are reportedly herbivorous (Fretter, 1939; Rudman, 1971a,b; Gibson and Chia, 1989). Diet and feeding behavior have been described for *H. hydatis* (Linnaeus, 1758) and *H. zelandiae* (Gray, 1843) (Fretter, 1939; Rudman, 1971a, b). Both species feed on filamentous green algae using the jaws and radula to break pieces of algae and the gizzard plates to grind them. This paper presents information on the dietary composition, changes in diet, and behaviors associated with the location and consumption of food by *A. canaliculata* and *H. solitaria*.

MATERIALS AND METHODS

Acteocina canaliculata and *Haminoea solitaria* were collected in summer 1989 and spring 1990 from a sandy-mud flat in Bluff Hill Cove, Point Judith Salt Pond, Galilee, Rhode Island, USA (41° 23'N, 71° 30'W) (Fig. 1). Qualitative field observations on the relative abundance of both snails were made approximately every month from April 1989 to September 1990.

Individuals for diet analysis were collected by passing the flocculent top 1 cm of substratum through a 1.0 mm sieve. The animals were fixed in 5% buffered formalin immediately after collection and transferred to 75% ethanol after 24 to 48 hours. The digestive tract of *Acteocina canaliculata* was removed with the aid of a dissecting microscope, and the contents spread on a microscope slide. Food items were transferred with the aid of a small camel hair brush to double-stick tape mounted on a microscopic slide. Items were identified to the lowest possible taxonomic level utilizing Loosanoff *et al.* (1966), Abbott (1974), Cushman (1976), and

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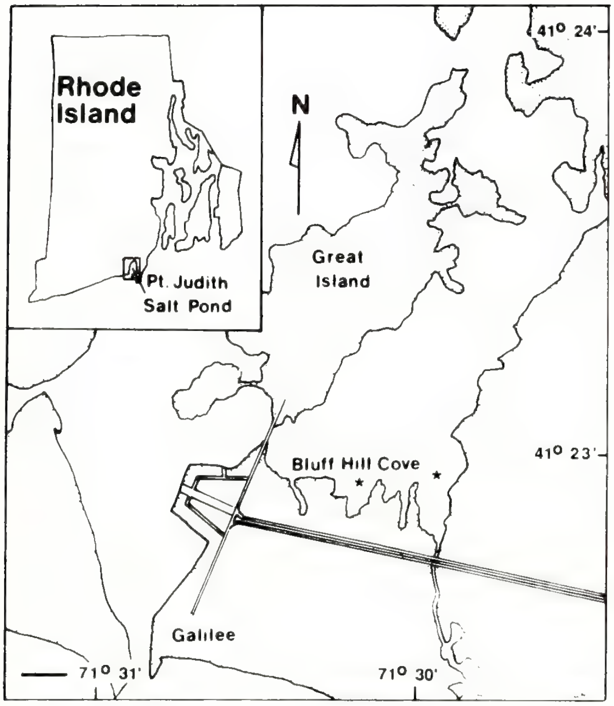

Fig. 1. Location of study site where *Acteocina canaliculata* and *Haminoea solitaria* were collected. Specific collecting sites are marked with an asterisk (scale bar = 200 m).

Todd and Low (1981).

Preliminary observations revealed that *Haminoea solitaria* feeds on diatoms and detritus. Therefore, the contents of the digestive tract were determined following the methods of Kesler *et al.* (1986). The digestive tract was removed, the contents mixed with a small amount of water, and evenly distributed on a glass slide. A grid containing 50 evenly spaced fields was viewed at 100x and scored for the presence of diatoms, filamentous algae, animal parts, sand, and detritus. The presence of each food type was quantified as the proportion of total fields containing that food item out of all fields that contained one or more food items. This procedure assumes that the proportion of fields containing an item reflects the amount of the food item in the diet. Items were identified utilizing Kennett and Hargraves (1988). Additionally, fecal remains from ten individuals were spread on a slide and viewed at 100x to determine which of the ingested material was being digested.

Multivariate analysis of variance (MANOVA) was performed on dietary proportions with respect to shell length and sample date (Sokal and Rohlf, 1981). Shell length of each animal was measured to the nearest 0.1 mm. Three size groups were chosen to give equal sample sizes between groups. Statistical analyses were performed using Statistical Analysis System (SAS Institute, Cary, NC). The results are presented as an F-ratio (F), with the appropriate degrees of freedom (d.f.), and level of significance (P).

Snails used for feeding observations were collected as above and maintained in small aquaria. Algal and sediment samples were taken at the same time and location as the snails in order to present the same potential food sources to the snail as are found in their natural habitat. Feeding behavior was recorded with a video camera, mounted so as to view the ventral region of the snail, and a video cassette recorder that allowed frame-by-frame analysis of behavioral events.

Potential food items of *Acteocina canaliculata* (foraminiferans and bivalves) were selected carefully from substratum samples and placed in small petri dishes. These prey organisms were acclimated to laboratory conditions for at least 24 hr prior to observations. Attempts were made to remove sediment particles clinging to foraminiferans to improve the clarity of viewing feeding activity. A variety of potential food items, including a thin layer of sand containing micro-organisms and various algal species found in the sediments at the mudflat, was presented to *Haminoea solitaria* in a small glass chamber (10 x 10 x 12 cm).

Voucher specimens of *Acteocina canaliculata* (MCZ 302559) and *Haminoea solitaria* (MCZ 302560), collected from the study site, are located in the collections of the Museum of Comparative Zoology (MCZ), Harvard University.

RESULTS

ACTEOCINA CANALICULATA

Acteocina canaliculata was present on the Bluff Hill Cove mud flat throughout 1989 and 1990, with the highest abundances occurring during July and August 1989. Larger snails (shell length > 3.9 mm) were more abundant during these two months (Fig. 2). Juveniles (shell length > 1.0 mm) first appeared in March and April 1990.

1. DIET

Sixty-eight percent of the snails (n = 97, 2.0-6.8 mm shell length) contained food particles (Table 1). Food remains, consisting of foraminiferans and bivalves, were found in the esophagus, gizzard, stomach, and intestine. Ninety-eight percent of the food remains in the stomach and intestine were crushed yet remained as discrete particles. Food remains found posterior to the stomach consisted mainly of shell or test fragments and fecal material. Sediment grains were found in only nine individuals. The gizzard plates of all dissected individuals showed no obvious sign of physical damage.

Foraminiferans found in the digestive tract belonged to three suborders: Textulariina, Miliolina, and Rotaliina. The majority of miliolid foraminiferans recovered from the digestive tract was crushed. Some fragments did allow generic identification. The remaining fragments were classified as "miliolid spp." due to the porcelaneous appearance of the

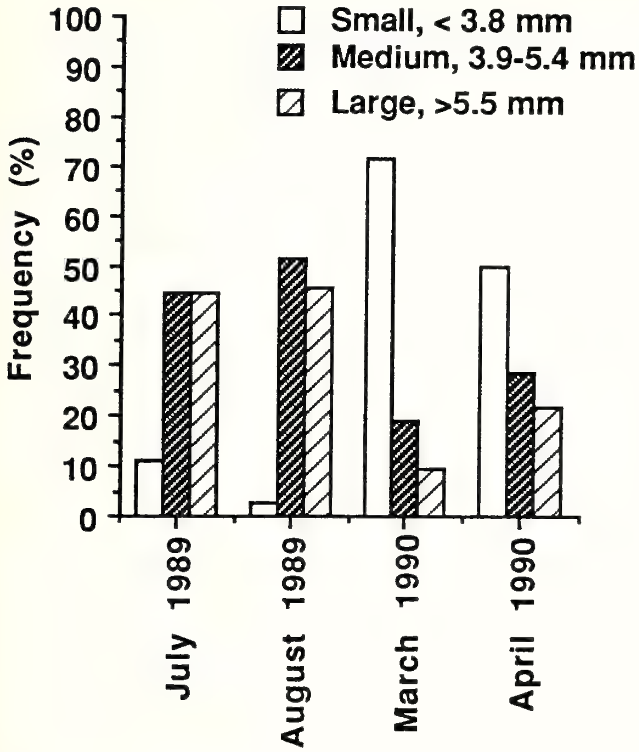

Fig. 2. Percentages of three sizes of *Acteocina canaliculata* collected over a four-month period from July 1989 to March 1990.

test (Todd and Low, 1981). Other foraminiferan fragments could not be identified and were classified as "unidentified forams." Eighty-three percent of Textulariina and Rotaliina found in the esophagus and gizzard were whole and showed no obvious signs of chemical or physical damage.

No bivalves were found in the esophagus, and all bivalves found in the gizzard, stomach, and intestine were crushed, making identification impossible in some cases. However, *Gemma gemma* (Totten, 1834) was usually identifiable based on the purplish coloration of its shell (Abbott, 1974).

Snail size was correlated with the type of food item in the gut (Fig. 3). The proportion of miliolid foraminiferans was signficantly lower in medium and large snails (MANOVA: F = 4.07, d.f. = 1, 61, P = 0.0481). In addition, there were fewer unidentified foraminiferan fragments in larger snails, probably an artifact because "fragments" taken from larger cephalaspids were larger and therefore more readily identifiable. A significantly higher abundance of bivalves was found in the guts of medium and large animals (MANOVA: F = 10.61, d.f. = 1, 61, P = 0.0018). In fact, only one animal < 5.0 mm had a crushed bivalve in its intestine.

The proportion of bivalves in the diet was significantly higher in July and August than in March and April (MANOVA: F = 12.44, d.f. = 1, 61, P = 0.0008) (Fig. 4). Unidentified foraminiferans were significantly higher in March than in other months (MANOVA: F = 4.33, d.f. = 1, 61, P = 0.0417). Again, this was probably due to the relative ease of identifying the larger foraminiferan fragments taken from larger animals.

2. BEHAVIORAL OBSERVATIONS: MOVEMENT

Movement was observed in 18 individuals (size = 3.6-5.2 mm). *Acteocina canaliculata* burrows into the top few millimeters of the substratum using the combined cephalic shield and tentacles as an efficient plow (Fig. 5). Sediment particles are carried by ciliary action along the dorsal surface of the cephalic shield and the posteriorly directed tentacles, and are sloughed off along either side of the shell. Typically, when moving, the head-foot extends forward, gliding across the substratum. With the foot extended anteriorly, the shell is retracted towards the head and the cycle repeated. Moving in this manner, the average speed for *A. canaliculata* was 17.6 mm per min on glass (n=3).

3. BEHAVIORAL OBSERVATIONS: FEEDING

A number of sense organs are located along the leading edge of the cephalic shield and foot. Two slightly darker sensory patches are located on either side of the mouth along the anterior edge of the cephalic shield (Fig. 6). Two other similar patches exist in corresponding positions on the foot. This area is highly active and was observed repeatedly touching the substratum and potential food items. Hancock's organs are located on either side of the head in antero-posterior grooves created by the cephalic shield and the foot. The animal characteristically swings the foremost part of the

Table 1. List of recovered food remains (including fragments) from 66 *Acteocina canaliculata* arranged by taxonomic group. % in Gut refers to the frequency of a food item in the gut. % Snails refers to the percent of snails in which a food item was present.

Food Item	% in Gut	% Snails	# of Particles
Suborder Textulariina			
Trochammina	23.7	57.4	77
Suborder Miliolina			
Miliommina	9.2	23.5	30
Quinqueloculina	8.3	27.9	27
Miliolid spp.	26.2	50.0	85
Suborder Rotaliina			
Pseudononion	2.2	7.4	7
Astrononion	1.9	7.4	6
Haynesina	0.6	2.9	2
Nonionella	0.3	1.5	1
Elphidium	0.3	1.5	1
Suborder Unknown			
Unidentified Forams	6.8	22.1	22
Class Bivalvia			
Gemma gemma	14.2	26.5	46
Unidentified bivalves	6.5	17.7	21

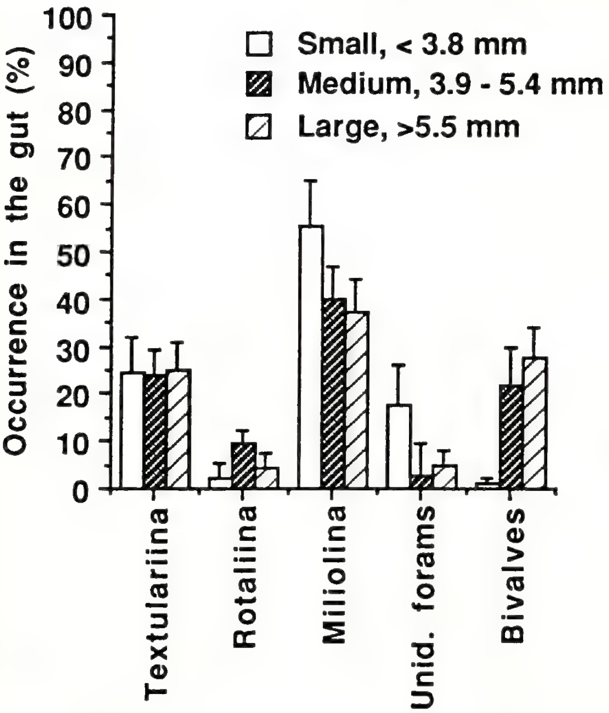

Fig. 3. Percentage of food items in the gut of three sizes of *Acteocina canaliculata* (bar = standard error of the mean).

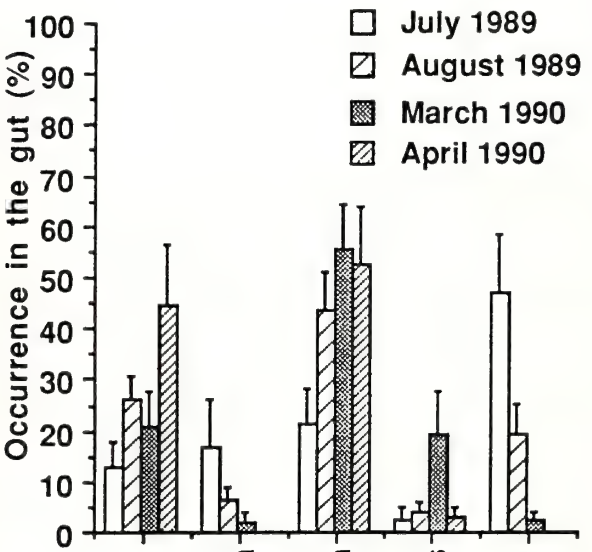

Fig. 4. Percentage of food items in the gut of *Acteocina canaliculata* collected in a four-month period from July 1989 to April 1990 (bar = standard error of the mean).

head back and forth, apparently searching for food. On six separate occasions, *Acteocina canaliculata* turned towards a prey items from a distance of 1 to 3 mm.

Feeding was observed in five individuals of *Acteocina canaliculata* (size = 4.5-5.2 mm). Upon contact, a potential food item is touched repeatedly by the sensory patches. The anterior edge of the cephalic shield and foot is compressed into a funnel-shaped cavity with the mouth in the center and sensory patches on either side. The mouth is then pressed against the food item, the buccal mass contracted, the odontophore protruded through the mouth, and the item gripped with the radula. The food item is then pulled into the buccal cavity. The jaws, located near the anterior end of the buccal cavity, appear to scrape off most of the sand grains clinging to the food item as it is drawn past the jaws into the mouth.

All foraminiferans ingested by *Acteocina canaliculata* were alive when eaten. Living foraminiferans are differentiated easily from empty tests because they are surrounded by detritus and sediment grains gathered by the reticulopodia (Cushman, 1976). Empty tests were ignored consistently by *A. canaliculata*, and they were passed up and over the cephalic shield along with sediment particles.

Capture and ingestion of a living bivalve *(Gemma gemma)* was observed only once. In this instance, a 5.2 mm snail turned towards the bivalve from a distance of 1.6 mm, and repeatedly touched it with its sensory patches. The bivalve was approximately 350 μm in height. It was gripped by the radula along the anterior edge, just anterior to the umbo, with the ventral opening facing down. Several attempts were made to draw the bivalve through the mouth and, after approximately two minutes, it was ingested.

HAMINOEA SOLITARIA

Haminoea solitaria was abundant seasonally, and it first appeared in mid-June 1989. The smallest individual collected during that summer was 3.0 mm in shell length. Field observations revealed that *H. solitaria* was extremely abundant during summer 1989, with large individuals more prevalent than small individuals in July and August. None were found after 17 November 1989. *H. solitaria* was first collected in 1990 on 13 July. The smallest individual collected during 1990 was 3.7 mm.

1. DIET

Sixty-seven percent of the snails (n = 106, 3.8-12.0 mm shell length) contained food items in their digestive system. Diatoms accounted for 36% and detritus accounted for 34% of the material ingested. Diatoms found included *Grammatophora, Thalassiosira, Coscinodiscus, Peridinium, Navicula, Gyrosigma, Skeletonema,* and *Chaetoceros.* Sand also constituted a large portion (26%) of the material found in the gut. Algae composed 3% of the diet. No attempt was

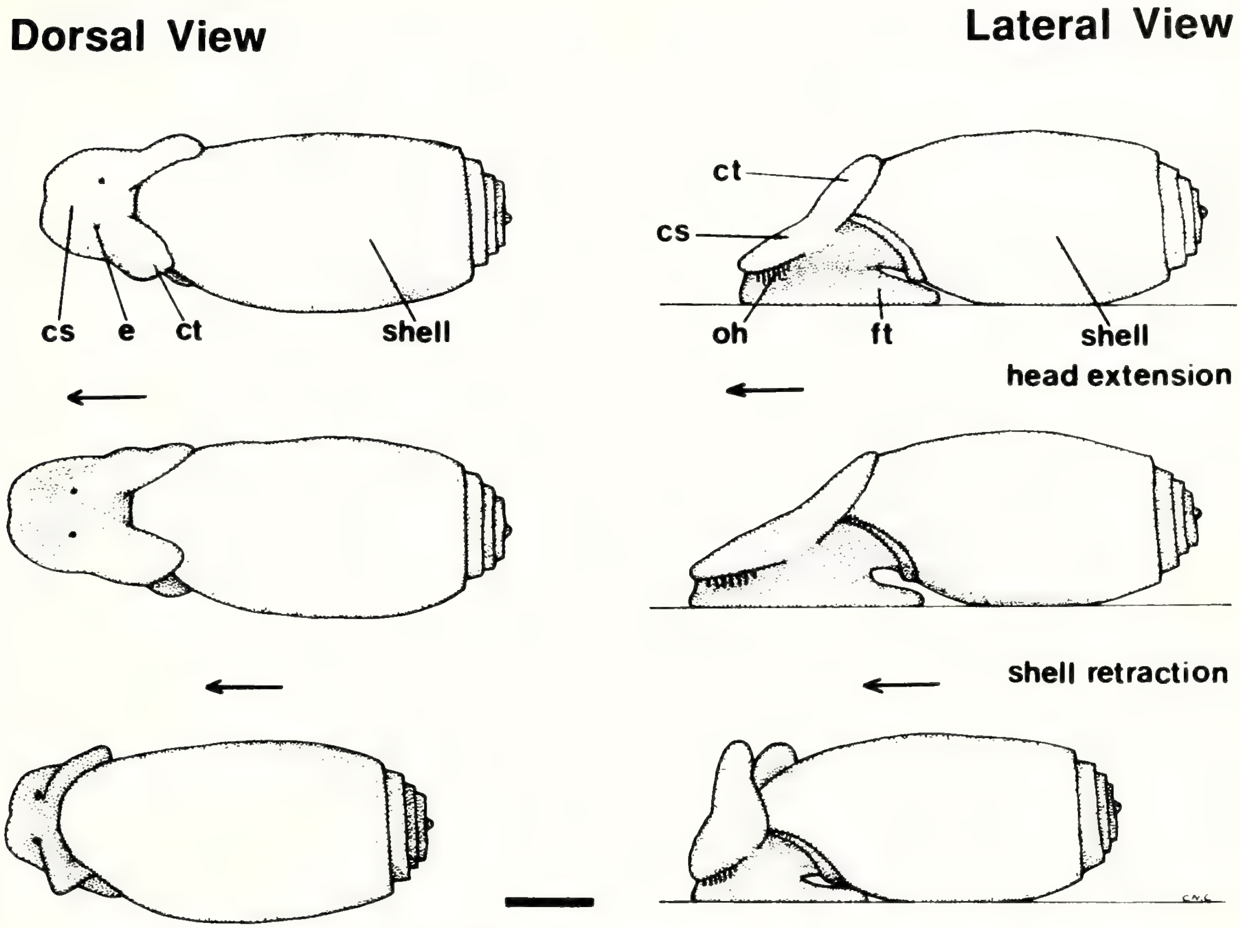

Fig. 5. Dorsal and lateral view of *Acteocina canaliculata* movement: cs, cephalic shield; ct, cephalic tentacle; e, eyespot; ft, foot; oh, Hancock's organ (scale bar = 1 mm).

made to identify algal species because of the small size of the fragments recovered. Additionally, a small fraction of the diet consisted of animals parts (1%). Animal parts included nematodes, copepods, nauplii larvae, ostracods, polychaete setae, oligochaetes, bivalves, and foraminiferans. The bivalves and foraminiferans showed no obvious signs of physical or chemical damage. Qualitative observations made of the fecal remains revealed that nearly all diatoms and animal parts consisted of empty tests suggesting that a large percentage of the diatoms and animals were digested.

The gizzard plates in 56 of the 106 *Haminoea solitaria* examined showed signs of damage. The outer, horny layer was usually torn away, creating pits in the plates. This was particularly apparent in larger individuals.

The proportion of sand and algae in the diet of *Haminoea solitaria* increased significantly with increasing snail size (MANOVA: sand, F = 10.43, d.f. = 1, 69, P = 0.0002; algae, F = 6.02, d.f. = 1, 69, P = 0.0166) (Fig. 7). Conversely, the amount of diatoms and detritus in the diet was significantly less in large animals (MANOVA: diatoms, F = 8.71, d.f. = 1, 69, P = 0.0043; detritus, F = 15.64, d.f. = 1, 69, P = 0.0002). There was no significant change in the proportion of animal remains in the diet of small and large snails.

The diet was highly variable among sample dates, even when the dates were only a few days apart. Significant differences existed between sample dates in the summer of 1989 for detritus, sand, and algae (MANOVA: detritus, F = 3.73, d.f. = 7, 69, P = 0.0019; sand, F = 4.53, d.f. = 7, 69, P = 0.0004; algae, F = 3.58, d.f. = 7, 69, P = 0.0026) but not for diatoms or animals parts (Fig. 8). The proportions of diatoms in the diet decreased over time. There was no apparent trend in detritus and sand, but the percent of algae did exhibit an increase through August, a drop at the end of August and at the beginning of September, followed by a subsequent increase during September.

2. BEHAVIORAL OBSERVATIONS: MOVEMENT

Movement was observed in 18 individuals of *Haminoea solitaria* (size = 3.3-11.2 mm). The foot of *H. solitaria* is

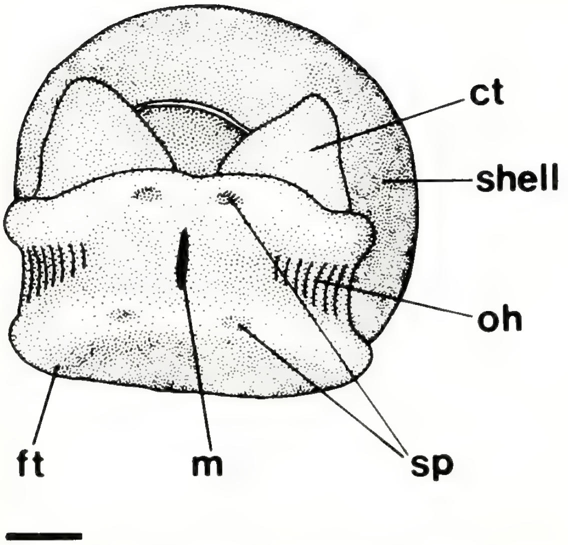

Fig. 6. Anterior view of *Acteocina canaliculata*: ct, cephalic tentacle; ft, foot; m, mouth; oh, Hancock's organ; sp, sensory patches (scale bar = 0.5 mm).

relatively larger than that of *Acteocina canaliculata* and has two parapodial lobes which curve up and around the anterior of the shell, often meeting mid-dorsally (Fig. 9a). Posterior to the foot, the floor of the mantle cavity extends posteroventrally beyond the shell, forming the posterior mantle lobe. When moving, *H. solitaria* glides smoothly through the substratum. The foot secretes an almost complete tube of mucus which helps prevent sediment particles from clogging the mantle cavity. Sediment particles are moved along the ciliated cephalic shield where they are entrapped in the mucous secretions of the foot and sloughed off posteriorly. *H. solitaria* moves much faster than *A. canaliculata*, traveling an average of 97 mm per min on glass (n=3).

3. BEHAVIORAL OBSERVATIONS: FEEDING

Hancock's organs are located on either side of the head in antero-posterior grooves created by the cephalic shield and foot (Fig. 9b). They are smaller than in *Acteocina canaliculata*, and consist of slightly wavy ridges. In addition to Hancock's organ, two sensory palps are located on either side of the mouth, also in the antero-posterior groove. Sensory patches were observed in a few individuals, but could not be consistently found in all animals that were observed. *Haminoea solitaria* swings its head back and forth while moving forward. The leading edge of the cephalic shield and foot is highly active and repeatedly touches anything with which the animal comes in contact.

Feeding was observed in seven individuals (size = 4.6-10.9 mm). The feeding behavior of *Haminoea solitaria* is similar to that of *Acteocina canaliculata*. The buccal mass contracts, the odontophore protrudes through the mouth, and the radula grasps a mouthful of sediment. The odontophore is then withdrawn and the buccal mass relaxes. All individuals observed appeared to ingest sediment at random with no selection of food particles. However, on several occasions *H. solitaria* rejected ingested particles by expectorating them.

DISCUSSION

Among opisthobranch gastropods, cephalaspids show the greatest diversity in feeding strategies, ranging from herbivores that graze algal mats or consume pieces of algae to carnivores that engulf whole prey animals (Kohn, 1983). The two species studied here have very different diets and exhibit two different feeding modes. *Acteocina canaliculata* seeks out and ingests whole foraminiferans and bivalves, while *Haminoea solitaria* consumes mouthfuls of sediment containing diatoms, detritus, and algae. Hard-shelled prey pass through *H. solitaria* apparently undigested.

In general, foraminiferans are ingested by two types of predators, unselective predators that ingest sediments containing foraminiferans, and selective predators that preferentially ingest foraminiferans (Lipps and Valentine, 1970; Murray, 1973). The diet and feeding behavior observed demonstrate that *Acteocina canaliculata* is a selective predator of foraminiferans in the sense that the snails are not selecting random sediment samples. Selective predation of forams

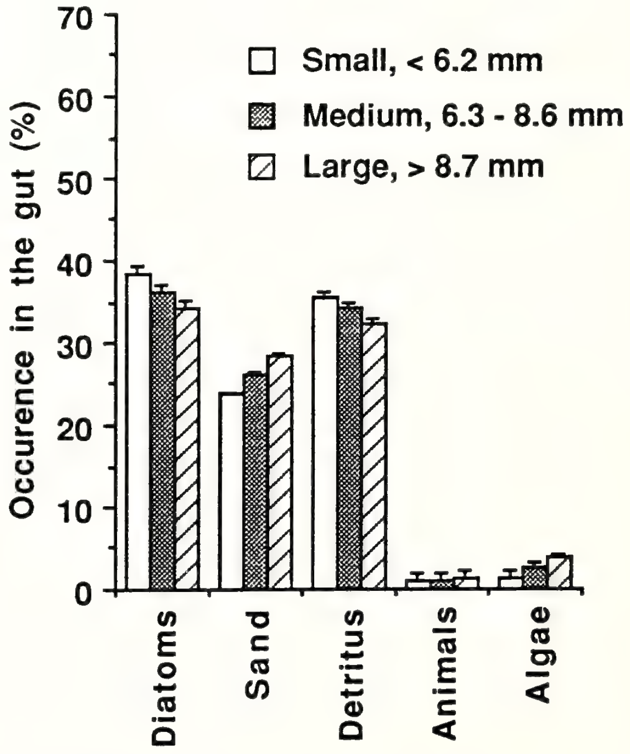

Fig. 7. Percentages of food items in the gut of three sizes of *Haminoea solitaria* (bar = standard error of the mean).

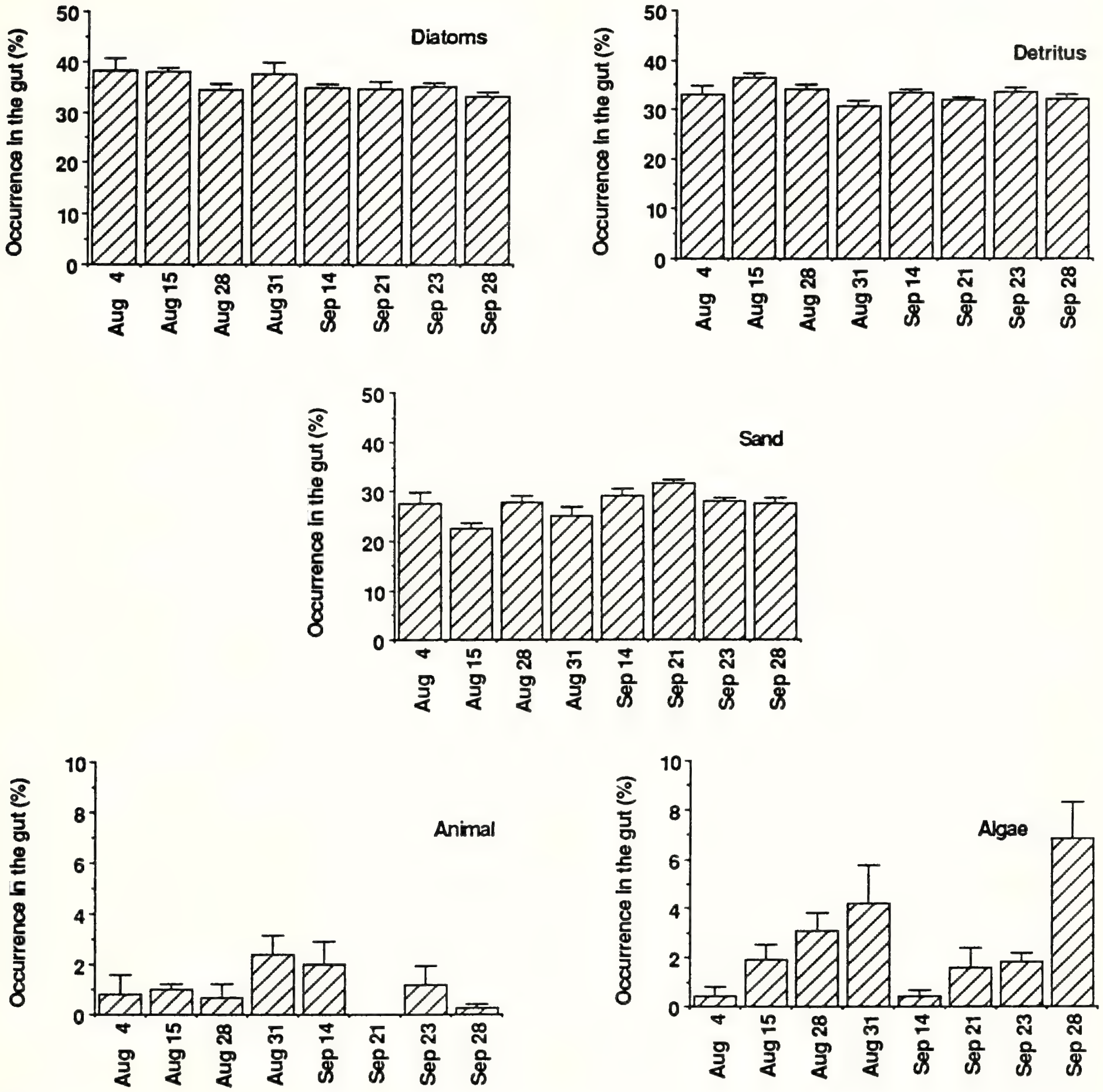

Fig. 8. Percentages of food items in the gut of *Haminoea solitaria* for eight sample dates in 1989 (bar = standard error of the mean).

has also been observed in *A. culcitella* (Shonman and Nybakken, 1978) and other cephalaspids (Hurst, 1965; Burn and Bell, 1974a,b; Berry, 1988; Berry and Thomson, 1990). These observations further suggest that *A. canaliculata* locates food items before they are physically contacted using Hancock's organ and sensory patches. Hancock's organ functions as a chemosensory organ in other cephalaspids (Lemche, 1956; Hurst, 1965; Edlinger, 1980; Kohn, 1983). Sensory patches have been observed in the genus *Philine* (Hurst, 1965; Rudman, 1972c). In *P. aperta* Linnaeus, 1766 they are believed to aid in prey location and capture (Hurst, 1965). These organs, in *A. canaliculata*, appear to play a specific role in food acquisition, that of locating individual foraminiferans. In *A. canaliculata*, sensory patches appear to play a similar role.

Ontogenetic changes in diet have been observed in other gastropods, as well as in seastars, chitons, and fish (Hurst, 1965; Hughes, 1980; Taylor, 1980; Berry, 1988; Paine, 1988; Berry and Thomson, 1990). The diet of *Acteocina canaliculata* changed with shell size. As size increased, the

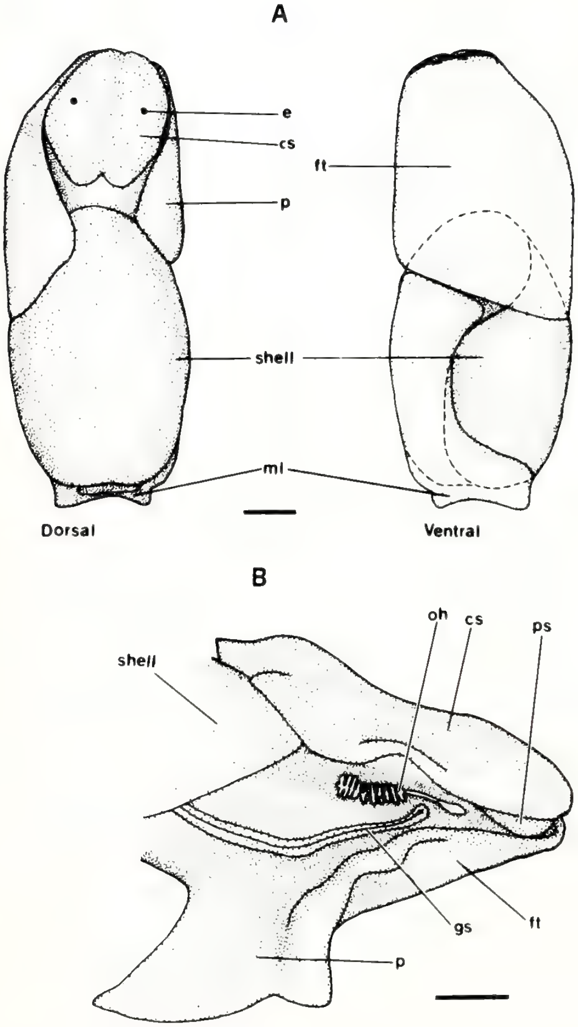

Fig. 9. External anatomy of *Haminoea solitaria.* A. Dorsal and ventral views (scale bar = 2 mm). B. Lateral view of head-foot with lateral parapodia reflected ventro-laterally (scale bar = 1 mm): cs, cephalic shield; e, eyespot; ft, foot; gs, external seminal groove; ml, posterior mantle lobe; oh, Hancock's organ; p, parapodial lobes; ps, sensory palps.

abundance of miliolid foraminiferans in the gut decreased. Additionally, there was an increase in the proportion of bivalves in the guts of snails larger than 5.0 mm. This dietary pattern could represent an inability of small *A. canaliculata* to ingest large prey items. Foraminiferan size is generally between 50 μm and 300 μm (Cushman, 1976). Bivalves are typically larger than 200 μm when they settle. For example, *Mya arenaria* Linnaeus, 1758, has a minimum shell size at metamorphosis of 225 x 209 μm (Loosanoff *et al.*, 1966), thus representing the smallest bivalve species that is potentially available to *A. canaliculata* at Galilee. Snails smaller than 5.0 mm in length could be restricted to ingesting only foraminiferans due to the size of their digestive tract. From about 5.0 mm shell length the diameter of the digestive tract or size of the radula would be large enough to allow *A. canaliculata* to incorporate bivalves, as well as larger foraminiferans, into its diet. Unfortunately, the number of measurable food remains was too small to adequately test this hypothesis.

A shell length of 5.0 mm could also represent a practical limit to the size at which the energy gained by eating foraminiferans is greater than the energy expended in searching for and ingesting them. Assuming that there is more energy to be gained by eating bivalves compared to foraminiferans, and that *Acteocina canaliculata* is maximizing its energy intake, then bivalves may be more profitable to snails larger than 5.0 mm (see Hughes, 1980).

A significantly higher proportion of bivalves was found in the diet of *Acteocina canaliculata* in July and August when larger snails were more common. This suggests that seasonality of prey species may be another factor in determining diet. This has been demonstrated in *Retusa obtusa* (Berry, 1988; Berry and Thomson, 1990) and other gastropod predators, such as *Conus, Thais,* and *Polinices* (Hughes, 1980, 1986). Unfortunately, no data concerning natural abundances and seasonality of the prey species at Galilee were made during this study.

In contrast with *Acteocina canaliculata*, the diet and feeding behavior of *Haminoea solitaria* revealed that it indiscriminately ingests sediments containing diatoms, algae, and detritus. No apparent selection of food items was observed, indicating that the sensory organs do not play as specific a role in food selection as they do in *A. canaliculata*. However, these organs could be more generally involved in locating patches of sand containing a high abundance of diatoms or other organic material, or not involved in feeding at all.

The diet of *Haminoea solitaria* changed with respect to both sample date and snail size. The indiscriminate feeding behavior observed in *H. solitaria* suggests that the abundances of specific food items in the diet should parallel their relative abundances in the habitat. As with planktonic diatoms, benthic diatoms show a definite seasonal cycle in abundance and species composition (Kennett and Hargraves, 1988). Typically, there is a spring bloom characterizing certain species, a low abundance during July, August or September, followed by a bloom in October characterizing other species. The trends observed in the diet of *H. solitaria* with respect to predator size and sample date might be the result of seasonal changes in abundance of prey species.

Future studies on these animals should concentrate on a number of areas. The diets of *Acteocina canaliculata* and *Haminoea solitaria* reveal the importance of food abundance and seasonal distribution in fulfilling dietary requirements. Additionally, the size of ingested food items appeared to be important in the diet of *A. canaliculata*. Future studies should examine not only the abundance of prey organisms in the environment, but the life cycle and size of ingested prey species to understand fully the relationships between predator and prey. Sensory organs appear to have a specific role in food acquisition in *A. canaliculata*, but the role of such organs in *H. solitaria* is unclear. Further research is necessary to determine more specifically the role sensory organs play in food detection and selection in these cephalaspids.

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Research Note

Comparative Morphology of the Byssi of *Dreissena polymorpha* and *Mytilus edulis*

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Abstract. Scanning electron micrographs reveal differences in byssal stems, threads and plaques of two common biofouling mussels, the zebra mussel *Dreissena polymorpha* (Pallas), and the blue mussel *Mytilus edulis* (Linnaeus). These differences include anchorage of the stem, the pattern in which threads branch from the growing stem, thread surface topography, plaque orientation, and the morphology of the region of the thread that extends into the plaque. Morphological dissimilarities are likely to be related to differences in the mechanics of byssus formation and to differences in the surface texture and length of the ventral groove. Morphological differences between byssi of various biofouling mussels should be considered as researchers develop and adapt mechanisms of control.

The post-larvae of most bivalve molluscs possess byssal structures by which they are secured to the substratum as they undergo metamorphosis (Yonge, 1962). Some bivalves retain a byssal apparatus into the adult stage. For example, the marine blue mussel *Mytilus edulis* (Linnaeus), which is well known for its commercial importance, and the freshwater zebra mussel *Dreissena polymorpha* (Pallas), a recent invader of the Great Lakes (see Mackie *et al.*, 1989 for a review of the zoogeography of *D. polymorpha*), are two species that retain a byssus as juveniles. Thus, the byssus plays a major role early in the lives of most bivalves and is important throughout the lives of some species.

Purchon (1977) lists two major advantages to the presence of a byssal attachment. First, by forming a byssal attachment, molluscs do not expend energy unnecessarily to maintain position on a substratum. In addition, when the tide ebbs or the water level falls, a byssate mollusc can withdraw its foot and close its shell valves to prevent desiccation. Mussels are, therefore, regarded as being among the most difficult fouling organisms to control because they are capable of withstanding conditions that eliminate most other species. For instance, chlorination has been used in attempts to control both *Mytilus edulis* and *Dreissena polymorpha*. Holmes (1970) reports that in *M. edulis*, one of the most serious offenders in fouling marine intake systems (Clapp, 1950), the principal effect of chlorination was a depression in the activity of the foot, leading to a reduction in the number of threads formed. In addition, chlorination interfered with the quinone tanning process of thread formation, so that the threads formed were weaker than those of unchlorinated animals (Holmes, 1970). Therefore, although chlorination created a flow dependent distribution of mussels due to weakening of their byssus attachment systems, chlorination failed to suppress fouling by *M. edulis* in areas of low water flow. In *D. polymorpha*, chlorination is effective in controlling zebra mussel larvae, but adult mussels are able to protect themselves from intermittent doses of chlorine by adduction (Anon., 1991).

Since zebra mussels were first identified in the Great Lakes as a two-year-old age class in 1988 (Hebert *et al.*, 1989), they have been causing fouling problems for users of raw water by accumulating on exposed surfaces and physically blocking intake pipes by attaching to one another to form layers as thick as 0.3 m (Clarke, 1952; Griffiths *et al.*, 1989). Because the zebra mussel contributes to the biofouling of water supplies primarily by forming byssal attachments, the study of byssus morphology could lead to the development of a method of controlling this mollusc.

It has been reported that the byssus of *Dreissena polymorpha* is similar to the byssal apparatus found in *Mytilus edulis* and other marine bivalves (Moore, 1991). In previous studies, however, the authors (Steele, 1991; Eckroat *et al.*, 1992) observed that the structure of the byssus of *D. polymorpha* differed from the byssal structure of *M. edulis* that had been described in the literature (Brown, 1952; Smeathers and Vincent, 1979). Therefore, the current study was undertaken to clearly delineate differences between the byssi of *D. polymorpha* and *M. edulis* by making morphological comparisons of their stems, threads, and plaques. Accurate comparisons are especially important because morphological differences between the byssi of various biofouling mussels should be recognized as researchers develop and adapt control mechanisms that affect the byssus.

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MATERIALS AND METHODS

Live specimens of *Dreissena polymorpha*, 2.1-2.5 cm in length, were collected at Lampe Marina on Presque Isle, Erie, Pennsylvania, during October 1990 and maintained in a 15°C freshwater aquarium for approximately one month, where they were fed 200 ml of an alga mixture (3 g of *Chlorella* spp. blended in 1 L of water) daily. Additional live specimens of *D. polymorpha*, 1.5-2.3 cm in length, were collected in Thompson's Bay on Presque Isle, Erie, Pennsylvania, during May 1991 and maintained in a 15°C freshwater aquarium overnight before their byssal threads were prepared for examination. Live specimens of *Mytilus edulis* measuring approximatelyt 1.0 cm and 5.0-6.5 cm were collected at Wachapreague, Virginia, and at Rye, New Hampshire, respectively, and maintained in a 24°C saltwater aquarium (31 ppt) for 14 days and fed marine *Chlorella* spp. daily as described above.

To prepare specimens for scanning electron microscopy, either the byssi were removed, or the mussels' shells were opened so that the byssi could be studied intact. Specimens were fixed in 5% glutaraldehyde in sodium phosphate buffer (pH 7.2) for 24-48 hours at 5°C, washed in buffer alone for 15 minutes, and dehydrated in a graded ethanol series. After specimens were critical point dried using carbon dioxide as the transitional fluid, they were mounted on aluminum stubs and sputter coated with gold-palladium. Specimens were examined and photographed with a Hitachi S-570 scanning electron microscope.

RESULTS

Scanning electron micrographs provided more detailed views of byssal structures that have been diagrammatically represented by other workers (Brown, 1952; Smeathers and Vincent, 1979). Comparisons between the byssi of *Dreissena polymorpha* and *Mytilus edulis* were limited to noting morphological differences because age differences of specimens make size comparisons of structures meaningless.

In intact specimens of *Dreissena polymorpha*, the byssal stem was concealed inside a collar-like structure that was continuous with the foot, and the region where the byssal threads branched from the stem was not visible (Fig. 1). The stem of *Mytilus edulis*, which emerged from a raised area at the base of the foot was, however, visible in intact specimens, and the locations at which the threads branched from the stem were exposed (Fig. 2). Additional observations showed that the ventral groove extended to the distal tip of the foot of *M. edulis*, but extended only about half the length of the foot in *D. polymorpha*.

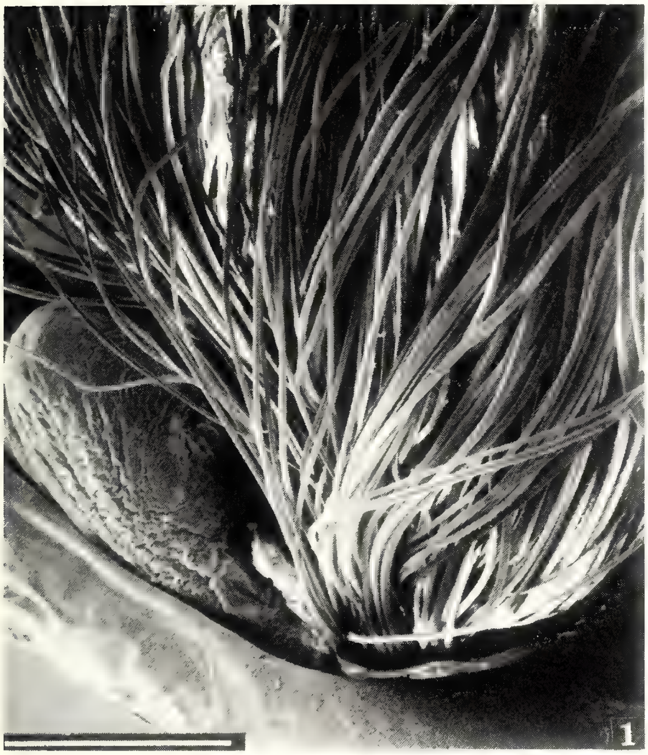
Removal of the byssus from specimens of *Dreissena polymorpha* revealed that most of their byssal threads branched from one linear location of the stem and from all around the stem's circumference (Fig. 3). Cuffs or sheaths, formed by the outer laminae, were observed at the bases of the threads in some specimens (Eckroat *et al.*, 1992). Examination of intact specimens of *Mytilus edulis* showed that threads, attached to the stem by overlapping rings, branched from progressively more distal locations along two opposite edges of the stem (Fig. 4).

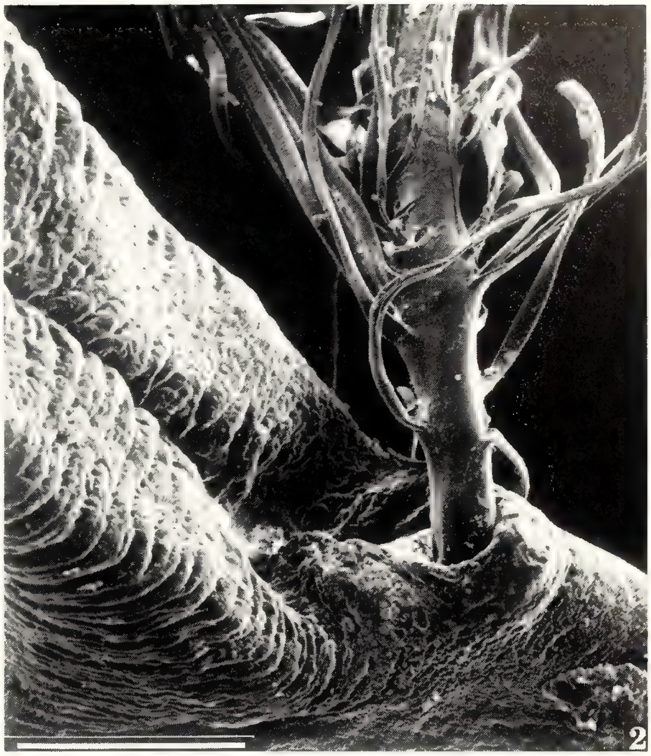
In the proximal region, threads of *Dreissena polymorpha* were cylindrical and smooth (Fig. 5), but the proximal portions of threads of *Mytilus edulis* were flattened with a crimped edge and had corrugations or folds around their circumferences (Fig. 6). The distal half of threads of *D. polymorpha* became increasingly rough with longitudinal ridges that were most pronounced at the distal ends of the threads (Fig. 7). Threads of *M. edulis*, however, were smooth in the distal region (Fig. 8).

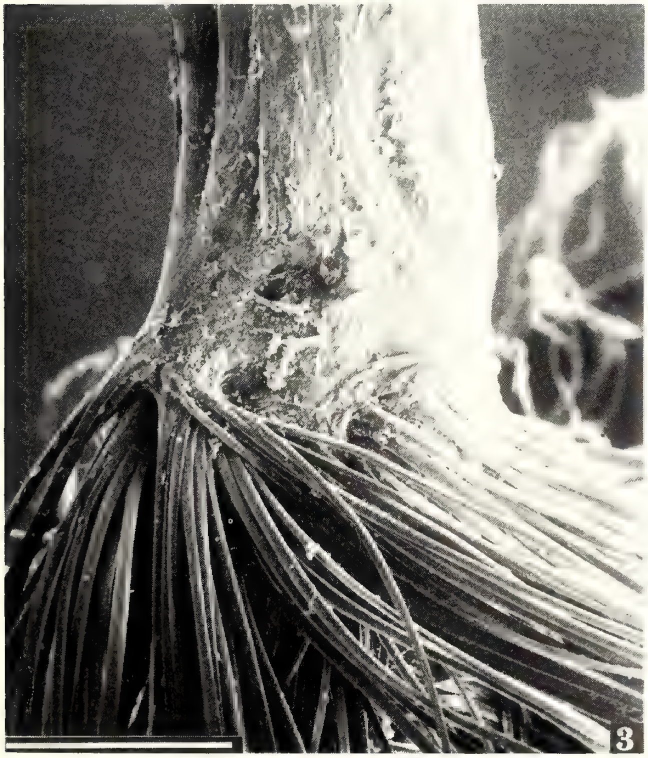
Threads of *Dreissena polymorpha* and *Mytilus edulis* formed oblique angles with the substratum and ended distally in thin, oval plaques (bottom portions of Figs. 9 and 10). In *D. polymorpha*, threads became broader, flattened, and bifurcated as they expanded along the plaque's wide axis (Fig. 9, near top), which was oriented perpendicular to the longitudinal axis of the thread (bottom portion of Fig. 9). Threads of *M. edulis*, however, trifurcated and formed thin, root-like extensions that continued into the plaque (top portion of Fig. 10). The narrow axis of the plaque was oriented perpendicular to the longitudinal axis of the thread (Fig. 10).

DISCUSSION

Byssus morphology is related to the mechanical events that occur during byssus formation. One of the first mechanical events involves the movement of the foot tightly against the substratum so that the mussel can secrete a plaque (Waite, 1983; Eckroat *et al.*, 1992), which is molded by the distal depression of the ventral groove of the foot (Brown, 1952; Waite, 1983). After a plaque has been formed, an individual thread, which is of a fluid consistency, is extruded from the ventral groove (Smyth, 1954; Waite, 1983). The plaques of *Mytilus edulis* and *Dreissena polymorpha* are very thin at their peripheral regions, but their orientations on the substratum differ. In addition, the structure of the portion of the thread that continues into the plaque is dissimilar in the two species. These differences in plaque orientation and distal thread morphology could result because the ventral groove does not extend to the distal tip of the foot in *D. polymorpha* as it does in *M. edulis*, which could affect the







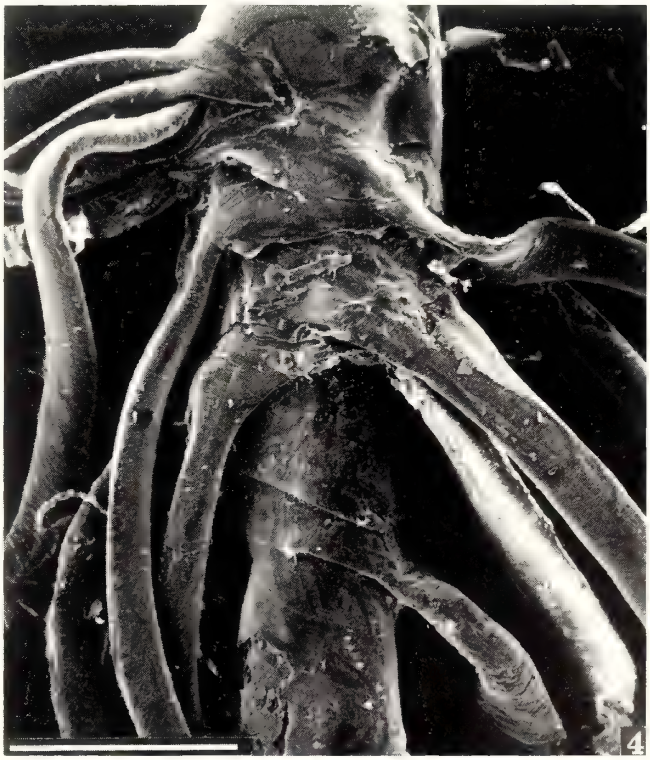
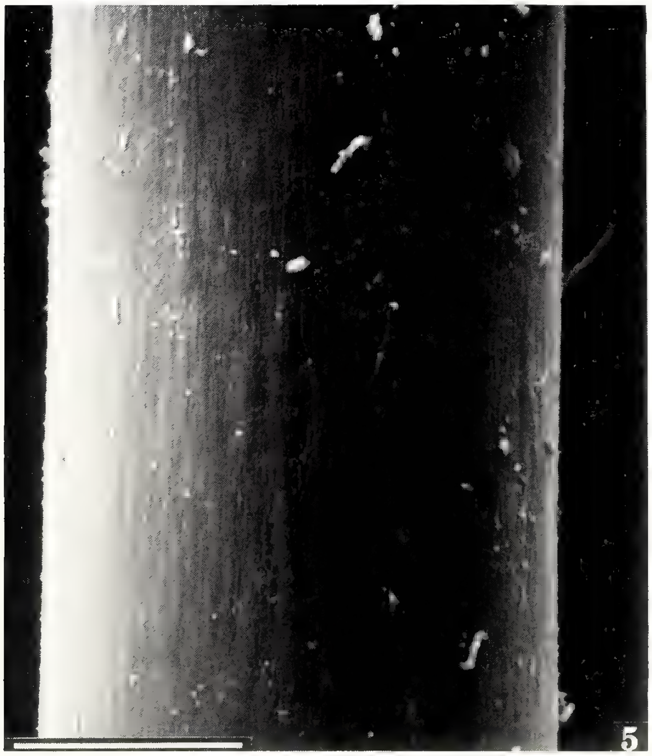
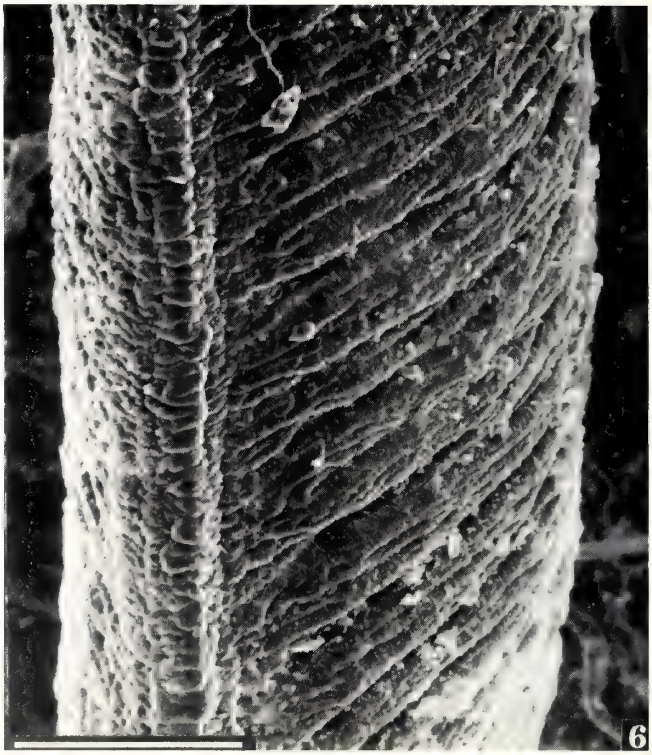
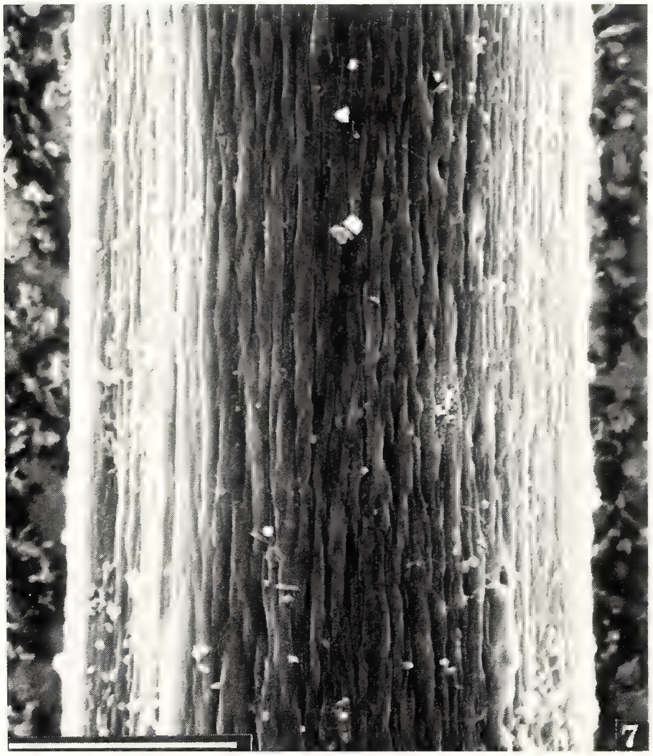


Fig. 1. Intact byssus of *Dreissena polymorpha* with threads emerging from a collar-like structure that conceals the stem (scale bar = 1.00 mm). **Fig. 2.** Intact byssus of *Mytilus edulis* with the stem emerging from a raised structure near the base of the foot (scale bar = 0.30 mm). **Fig. 3.** Stem of *D. polymorpha*. Threads branch from around the circumference of one proximal-distal location of the stem (scale bar = 0.60 mm). **Fig. 4.** Stem of *M. edulis*. Threads branch from progressively distal regions along two opposite sides of the stem and are attached by overlapping rings (scale bar = 0.50 mm).







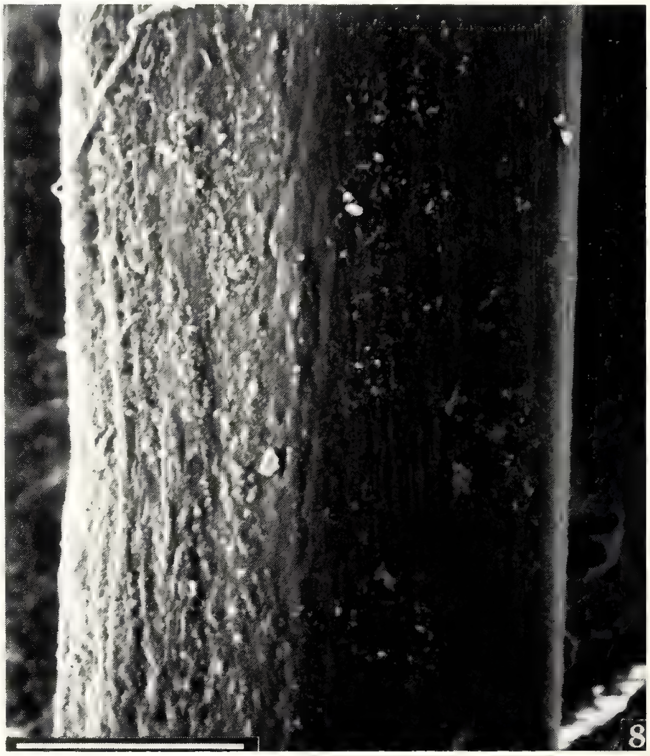


Fig. 5. Smooth, proximal portion of thread of *Dreissena polymorpha* (scale bar = 10.0 μm). **Fig. 6.** Flattened proximal portion of thread of *Mytilus edulis* with crimped edge and folds around circumference (scale bar = 43.0 μm). **Fig. 7.** Distal portion of thread of *D. polymorpha* with longitudinal ridges (scale bar = 23.1 μm). **Fig. 8.** Smooth, distal portion of thread of *M. edulis* (scale bar = 38.0 μm).

shape of the distal depression as the foot is pressed against a substratum. In addition, differences could arise in the shape of the distal depression that could affect the morphology of the distal ends of the threads if the muscle action of the foot differs in the two species.

As threads are secreted as a liquid, they are molded to the walls of the ventral groove (Brown, 1952; Smyth, 1954; Bairati and Vitellaro-Zuccarello, 1974; Waite, 1983). Our results, which agree with those of other workers (Brown, 1952; Smeathers and Vincent, 1979), show that the threads of *Mytilus edulis* are corrugated in the proximal third and smooth in the distal two-thirds. The threads of *Dreissena polymorpha*, which are smooth in the proximal half and rough with longitudinal ridges in the distal half, therefore, differ from those of *M. edulis*. These thread surface differences suggest that the walls of the ventral groove of *D. polymorpha* have a different surface topography than those of *M. edulis*.

Once a thread has been completed, specimens of *Mytilus edulis* change position and repeat the process to form another thread (Clapp, 1950). The changes in position made by *Dreissena polymorpha* and *M. edulis* could differ because in the two species, the patterns in which the threads branch from the stem differ. In *D. polymorpha*, threads branch from around the circumference of the stem, but in *M. edulis*, threads branch from two opposite sides.

The ways in which the threads of the two species are attached to the stem are dissimilar. Our observations agree with those of Brown (1952), who reported that the threads of *Mytilus edulis* are attached to the byssus with overlapping rings that are fused with the fibrous laminae of the byssal root, while the threads of some *Dreissena polymorpha* specimens have cuffs at their bases (Eckroat *et al.*, 1992). Unlike the threads of *M. edulis*, which branch from progressively distal locations along the stem, threads of *D. polymorpha* branch from the stem at one linear location. Brown (1952) explained that in *M. edulis*, as the fibrous laminae of the root increase in length, the stem lengthens and older threads are carried farther from the body of the organism. The thread branching pattern observed in *D. polymorpha*, however, suggests that as threads are added to the byssus, the stem does not lengthen in the region where the threads branch. New threads are attached to the outside of the stem, which increases stem diameter but not stem length.

The byssi of *Dreissena polymorpha* and *Mytilus edulis* differ in the anchorage of the stem, the pattern in which threads branch from the growing stem, thread surface topography, plaque orientation, and the morphology of the region of the thread that extends into the plaque. Therefore, although previous reports (Moore, 1991) stated that the byssi of these molluscs were similar, marked structural differences exist. Because byssal attachment is fundamental to the success of mussels that colonize hard substrata, information concerning structural characteristics of the byssus could be used together with knowledge of thread formation and attachment to develop or adapt mechanisms of controlling biofouling mussels. It is therefore important to realize that among different molluscan species, the byssal apparatus has diverse designs. As control mechanisms are proposed, researchers should recognize such morphological dissimilarities and the possible differences in the mechanics of byssus formation that they could reflect.

ACKNOWLEDGMENTS

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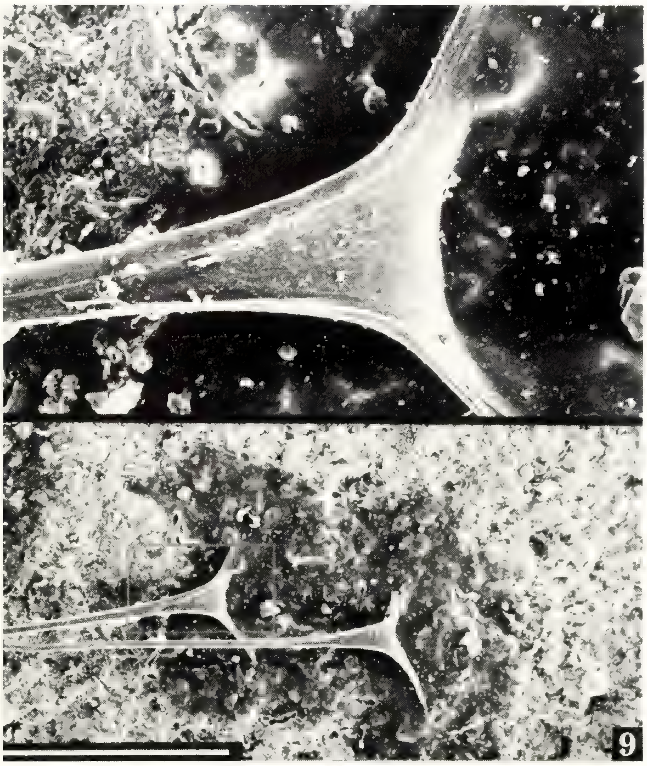

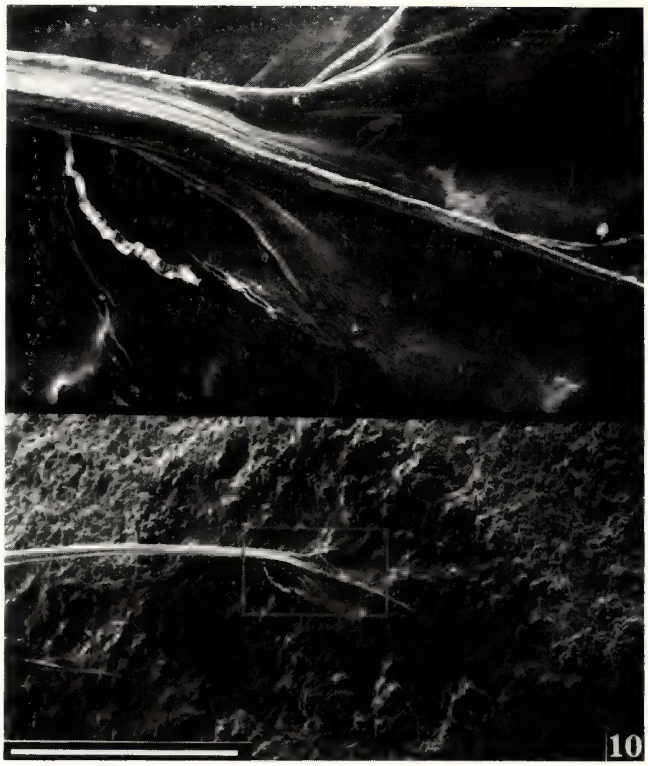

Fig. 9. Plaque of *Dreissena polymorpha* oriented with its wide axis perpendicular to the longitudinal axis of the thread in perpendicular vertical planes (bottom - scale bar = 0.43 mm). Broad, flattened portion of thread expanding along wide axis of plaque (top - scale bar = 86.0 mm). **Fig. 10.** Plaques of *Mytilus edulis.* The narrow axis of each plaque is perpendicular to the longitudinal axis of the thread to which it is attached (bottom - scale bar = 1.0 mm). Thin, root-like extensions spreading into plaque (top - scale bar = 0.20 mm).

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BOOK REVIEW

Zoological Catalogue of Australia, Vol. 8. Non-Marine Mollusca

Brian J. Smith, Australian Government Publishing Service. 1991. 405 pp. Austr. $49.95.

A new checklist of Australian non-marine molluscs has been published, almost 50 years after Iredale produced the last checklists dealing with these animals. This work has been the product of Brian Smith's labours over many years - he admits to 10 years in the introduction - during which time Australian malacologists eagerly awaited its completion.

There could be few more tedious occupations than producing a checklist, especially one with the detail required in the Zoological Catalogue of Australia, of which this work is volume 8. The work lists over 2,000 available species names, over 1,000 of these recognised as valid species names, placed in about 400 genera in 57 families. These figures also include taxa restricted to brackish water - marginal marine groups (e.g. Ellobiidae, Assimineidae). Smith estimates that 30-40% of the Australian non-marine fauna remains undescribed.

The work itself suffers somewhat from being forced into an editorial straight jacket for which the author is not responsible. It was designed for terrestrial vertebrate checklists and the limitations of what apparently was an antiquated data base system. For example all references are spelled out in full - yes, really in full - title as well as a journal reference and the usual pagination, etc. every time a reference is cited - even if it appears several times on the one page (as is often the case). Needless to say this curious policy makes the work more voluminous than it otherwise might have been. In addition the rigid format does not allow remarks under genera or species - only under families, with the result that important comments relating to particular genera or species are easily overlooked. It is also unfortunate that available names that can without doubt be placed in a genus, but cannot be readily assigned to "valid" species as synonyms, or reliably treated as a "valid" species in their own right, are not listed under the genus but in a ragbag of *"incertae cedis"* at the end of the family.

This work is important and timely, not just because it's a useful reference to the fauna, but because it's the only reference that we have that gives us anything like a real picture of the diversity of non-marine molluscs in Australia. Given Smith's estimate of 1,000 valid species, with 30-40% undescribed, gives a total fauna of 1,300-1,400 species (some estimates suggest 2,000), dispelling the myth that the Australian non-marine molluscan fauna is relatively depauperate.

Because many genera are in a chaotic state taxonomically, a number of taxonomic decisions have been made in this work, some in conjunction with other workers. This work will be a valuable addition to the library of anyone with an interest in non-marine molluscs - and essential to anyone working with the Australian fauna.

—Winston Ponder
Australian Museum
Sydney NSW 2000
Australia

59th ANNUAL MEETING
THE AMERICAN MALACOLOGICAL UNION
ABOARD THE *NORDIC EMPRESS* WITH STOPS AT
FREEPORT, NASSAU, AND COCOCAY
BAHAMAS
JUNE 21- 25, 1993

Following the traditional format, the meeting will include a symposium, featuring patterns of speciation in molluscs, contributed papers sessions on diverse aspects of molluscan biology, field trips to various islands, and an auction of publications and other items of malacological interest. The Bahamian Islands provide unique opportunities for biologists to study and compare tropical insular faunas with the temperate faunas of North America, as well as providing an exciting and unforgettable workshop for family members and conference attendees alike.

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The *American Malacological Bulletin* serves as an outlet for reporting notable contributions in malacological research. Manuscripts concerning any aspect of original, unpublished research, important short reports, and detailed reviews dealing with molluscs will be considered for publication.

Each original manuscript and accompanying illustrations must be submitted with two additional copies for review purposes. Text must be typed on one side of 8½ x 11 inch bond paper, double-spaced, and all pages numbered consecutively with numbers appearing in the upper right hand corner of each page. Leave ample margins on all sides.

Form of the manuscript should follow that outlined in the *Council of Biology Editors Style Manual* (fifth edition, 1983). This can be purchased from the CBE, 9650 Rockville Pike, Bethesda, Maryland 20814, U.S.A.

Text, when appropriate, should be arranged in sections as follows:

1. Cover page with title, author(s) and address(es), and suggested running title of no more than 50 characters and spaces. Authors should also supply five key words, placed at the base of this page, for indexing purposes.
2. Abstract (less than 5% of manuscript length)
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5. Literature cited
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All binomens must include the author attributed to that taxon the first time the name appears in the manuscript [e.g. *Crassostrea virginica* (Gmelin)]. This includes non-molluscan taxa. The full generic name along with specific epithet should be written out the first time that taxon is referred to in each paragragh. The generic name can be abbreviated in the remainder of the paragraph as follows: *C. virginica.*

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Hillis, D.M. 1989. Genetic consequences of partial self-fertilization on population of *Liguus fasciatus* (Mollusca: Pulmonata: Bulimulidae). *American Malacological Bulletin* 7(1):7-12.

Seed, R. 1980. Shell growth and form in the Bivalvia. *In: Skeletal Growth of Aquatic Organisms,* D.C. Rhoads and R.A. Lutz, eds. pp. 23-67. Plenum Press, New York.

Yonge, C.M. and T.E. Thompson. 1976. *Living Marine Molluscs.* William Collins Son & Co., Ltd., London. 288 pp.

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EDITORIAL COMMENT

Volume 10(2) of the *American Malacological Bulletin* will measure ten years of my efforts as Editor of the official AMU journal publication. During this time I have had the distinct pleasure and honor of working with some of the best malacologists and biologists that our times have to offer. The joint efforts of our Board of Editors, Board of Reviewers, innumerable reviewers, authors, various AMU Councils and Publication Committees, and uncounted AMU members, have led to a journal that has grown in quality and distribution. With this issue I will terminate my Editorship of the *Bulletin* knowing that the dedication of these numerous individuals and groups will keep our AMU journal thriving through years to come. I would like, however, to personally acknowledge some individuals that put in more than their fair share of time and consistently helped navigate the success of our journal.

The Editorial Board for Volume 1 of the *American Malacological Bulletin*, published in May 1983 by Braum Brumfield Press, was intimately involved with the development of the journal. That Board, composed of M. R. Carriker, G. M. Davis, A. J. Kohn *(ex officio)*, R. Robertson, and W. D. Russell-Hunter, set the tone and pace for the journal. George Davis kindly took a great deal of his valuable time to meet with me at the Academy of Natural Sciences to give me "an inside look" at how a successful journal is run. I owe Louise Kraemer a special note of thanks for her early encouragement and unending patience. George Davis, Louise Kraemer and Mel Carriker offered tremendous support to my fledgling editorship. Gus Russell-Hunter and Robert Robertson were a steady source of good advice and support. Mel Carriker served as Chair of the Editorial Board and made sure our annual meetings ran smoothly and efficiently. Through the years others served on the Editorial Board, in *ex officio* capacity as President of the AMU, and I thank each for their time and energy. In 1988 Thomas Waller joined the Editorial Board and brought with him his enthusiasm, characteristic good sense and dedication to malacology. Tom now serves as Chair of the Editorial Board.

Up through volume 4(2) I acted as sole Editor of the *Bulletin*. At that time, however, the journal had grown to a point where I could no longer handle day to day operation of the review process, copy editing, and finances of the journal, and maintain a faculty position, without assistance. The finances were confidently turned over to the Treasurer of AMU, Anne Joffe. The role of copy editing and acting as general liaison with our printer fell to our Managing Editor, Ronald B. Toll. To Ron I owe a great deal of thanks for his willingness to serve, and serve with distinction. As the newly elected Editor-in-Chief, Ron brings his experience to insure the progress and growth of our journal.

In 1985 we moved to Shaughnessy Printers and have remained with them ever since. Denny Shaughnessy has provided many kind suggestions for our "book" and helped insure a quality "product". Carol Underwood's spirited production of the *Bulletin* through all phases of publication and her efforts, especially to meet last week's deadline, have been greatly appreciated. On the institutional homefront, many thanks for the very professional aide of Deena Kelly and especially Linda Andrew who managed a continuous flow of correspondence and helped me maintain my own deadlines. Indiana University of Pennsylvania and the University of Southern Mississippi supported our AMU journal by making time, supplies, phone lines, mailing, and most importantly, secretarial assistance continually available.

I have, for ten years, been able to continue with the Editorial responsibilities of the *Bulletin*, and carry on some semblance of an academic career, only because of the understanding, caring, encouragement, and positive outlook of my wife, Fran P. Prezant. Additional special thanks are extended to Connie Boone, Paula Mikkelsen, Bill Lyons, Dick Petit, Anne Joffe, Ray Neck, and the late Alan Solem and Dee Dundee for their support and encouragement, and for their dedication to and hopes for AMU and its journal. To all reviewers of manuscripts, and they number over 250 as listed in this issue, thank you for your time and stamina. The continued support of the American Malacological Union in building a professional journal with international credentials, speaks for itself as we close a decade of *Bulletin* publication. We can look forward with confidence to the continued growth of the American Malacological Union and our AMU journal.

Robert S. Prezant
July 1993

REVIEWERS FOR THE *AMERICAN MALACOLOGICAL BULLETIN*
VOLUMES 1 - 10
1983 - 1993

Publication of volume 10(2) of the *American Malacological Bulletin* represents the tenth anniversary of the official journal publication of the American Malacological Union. During this decade the journal expanded from one to two issues per year, and from the national to the international realm. The success of the *Bulletin* is directly attributable to the quality control exerted by the numerous reviewers we have used over the years. All of these individuals contributed to the growth of the AMU journal. The editors of the *Bulletin* would like to thank each reviewer for their dedication and professionalism through the years.

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Anatomy and systematics of a new species from China, *Aegista laoyelingensis* (Stylommatophora; Bradybaenidae)

Lu Zhang*

Department of Biology, Northeast Normal University, Changchun, Jilin, The People's Republic of China

Abstract: This paper describes a new species of pulmonate land snail, *Aegista laoyelingensis*, from Jilin Province, Northeastern China. The shell of this gastropod is small, light brown, unbanded, and has a rough surface. Whorls number about 5.5 ± 0.1; the last whorl is never keeled. *Aegista laoyelingensis* has a short epiphallus, but lacks a flagellum. This species has a unique pattern of fusion of the central nervous system, and there is variation in mantle pigmentation.

The Bradybaenidae are a large, widespread family of pulmonate land snails with a distribution centered in Southeast Asia but ranging to Europe and North America. The Bradybaenidae comprise the following subfamilies: Aegistinae Kuroda and Habe, 1951; Bradybaeninae Pilsbry, 1924; Euhadrinae Minato, 1988; Helicostylinae Ihering, 1909; and Monadeniinae Nordsieck, 1987 (see Miller and Naranjo-Garcia, 1991). Over 80 genera and subgenera are involved (Richardson, 1983). The species of *Aegista* are common snails distributed in China, Japan and nearby Islands. There are about 33 Chinese species of *Aegista* described by Heude (1882), Tryon (1888), Pilsbry (1895), Wiegmann (1900), Yen (1939), Chen and Gao (1987). Unfortunately, these authors based their descriptions solely on shell characters; they did not supply anatomical data. The purposes of the paper are: (1) to describe a new species from Northeastern China, *Aegista laoyelingensis,* and present the detailed anatomy of the new species; (2) to document the variation in mantle pigmentation; (3) to discuss the classification of the Aegistinae.

MATERIALS AND METHODS

Specimens were collected from a small area of Laoyeling (Mountains), Jilin Province, the People's Republic of China, kept in jars filled with fresh leaves, and brought back to the laboratory of Northeast Normal University. After 5 hr, the living snails were drowned in distilled water for about 24 hr and allowed to fully extend. The specimens were fixed in 95% ethanol for about 1 hr, and then transferred to, and preserved in, 70% ethanol. Five adults of the alcohol-preserved specimens were dissected, and organs measured at the Academy of Natural Sciences of Philadelphia, using a Wild M5A dissecting microscope. Scanning electron microscope studies on the radula were done at Northeast Normal University, and photographed with a Hitachi scanning electron microscope. The internal structure of the penis, ganglia and mucous gland were observed by cutting and opening the outside wall surrounding these organs. Institutional abbreviations are as follows: ANSP, Academy of Natural Sciences of Philadelphia; NNUC, Northeast Normal University of China.

SYSTEMATICS

Family: Bradybaenidae Pilsbry, 1934
Genus: *Aegista* Albers, 1850
Aegista laoyelingensis Zhang sp. *nov.*

Type locality. Laoyeling (Mountains), Tiangang commune, Panshi County, Jilin Province, the People's Republic of China, 43.20° N, 127.40° E, on the bottom of a hill close to a railway station (about 2.5 km to the North of the station) elevation between 700 and 800 m.

Specimens were collected by the author on 16 July 1987. Habitat for the snails was a narrow area between a small stream and a trail. The main vegetation of the habitat was composed of the following trees: *Quercus, Populus, Juglans* and *Acer*; and bushes: *Corylus, Eleutherococcus* and *Lespedeza*. *Aegista laoyelingensis* preferred to crawl on the tops of bushes, with most snails collected from the leaves of *Corylus* and *Juglans* growing beside the stream.

Etymology. Named for the Mountains.

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MORPHOMETRICS

Holotype: shell height, 6.6 mm; shell diameter, 13.1 mm; whorls 5.6. (Fig. 1, NNUC 87001, preserved at the Institute of Zoology, Academia Sinica, Beijing, China.)

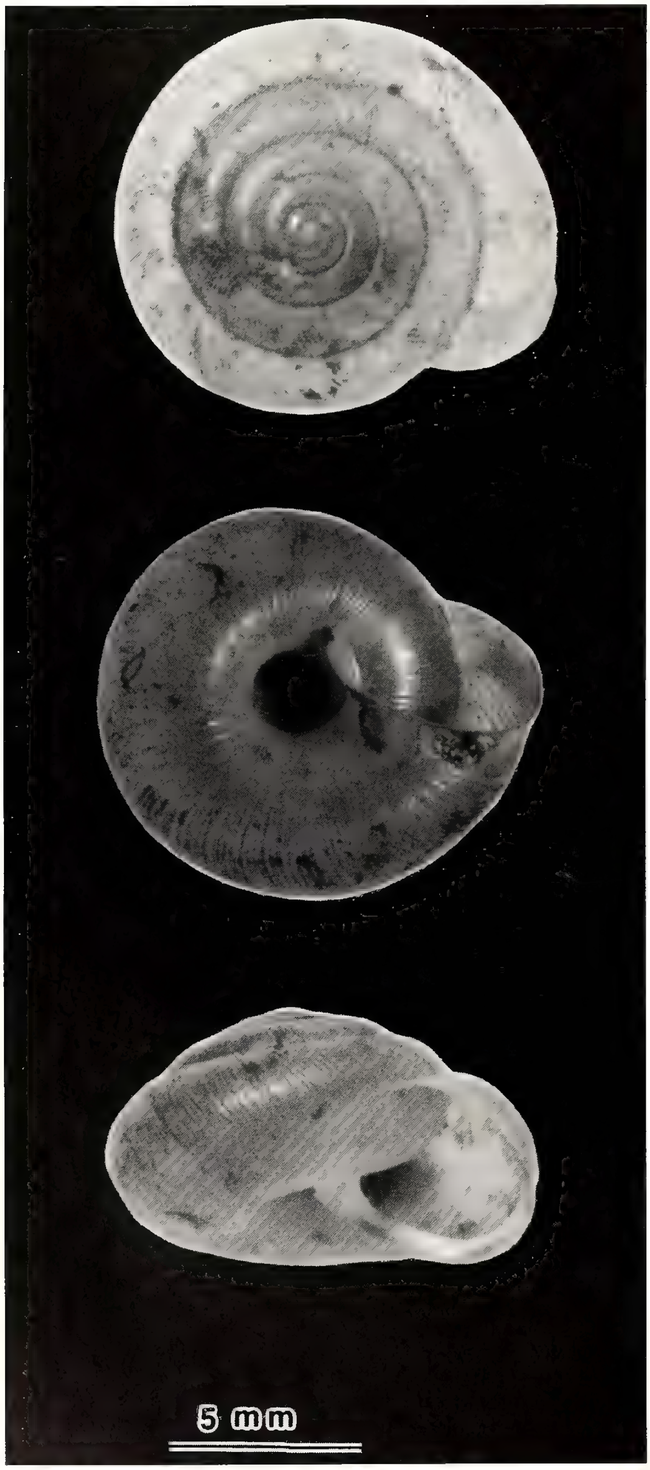

Fig. 1. Three views of holotype of *Aegista laoyelingensis.*

Paratype 1: shell height, 7.1 mm; shell diameter 14.3 mm; whorls 5.6, NNUC 87002.

Paratype 2: shell height, 6.3 mm; shell diameter 12.5 mm; whorls 5.5, ANSP 391682.

Paratype 3: shell height, 6.5 mm; shell diameter 12.9 mm; whorls 5.6, (in author's collection).

Paratype 4: shell height, 5.6 mm; shell diameter 11.1 mm; whorls 5.6, ANSP 391683.

DESCRIPTION

Shell. Shell small, depressed, with an open umbilicus, about 1/5 of shell diameter; shell light, somewhat thin, but solid; semitranslucent, uniformly light brown, not banded, whorls 5.6, surface often roughened by irregular growth lines. Spire low, with horn-colored apex, and with distinctly impressed suture. Body whorl not keeled or angulated, quite large in proportion; descending anteriorly. All whorls visible in the umbilicus and internal sutures deep. Aperture lunar, the peristome thin, colorless and toothless; narrowly reflexed at base.

Mantle. Mantle cavity length 26.9 mm. Mantle colors of holotype and paratype 1, 3 and 4 are lightly colored form, there is no pigmentation from the collar to the epithelium covering the uppermost part of the kidney (Fig. 2A). Variation in mantle pigmentation was found in paratype 2. The mantle is dark, the speckled melanin pattern can extend to the epithelium covering the uppermost part of the kidney (Fig. 2B).

Radula. Radula formula (from two individuals) is: $\frac{23\text{-}10\text{-}1\text{-}10\text{-}23}{68}$. (1 central tooth; 10 lateral teeth; 23 marginal teeth; 68 rows)

Each central tooth consists of two distinctly pointed cusps (Fig. 3b: 1). There is one cusp on the outside edge of

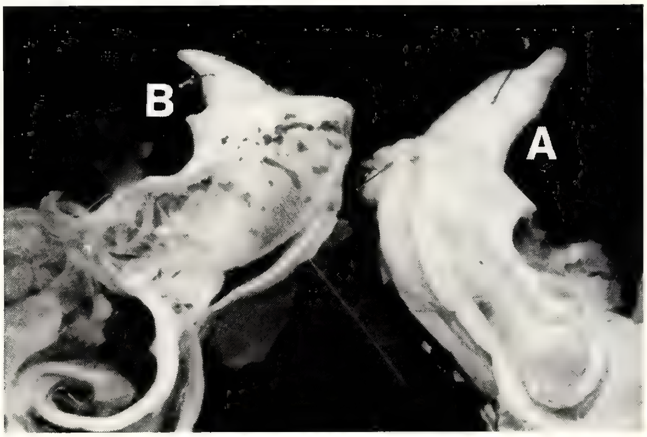

Fig. 2. Variation in mantle pigmentation. A, light form; B, dark form (speckled form).

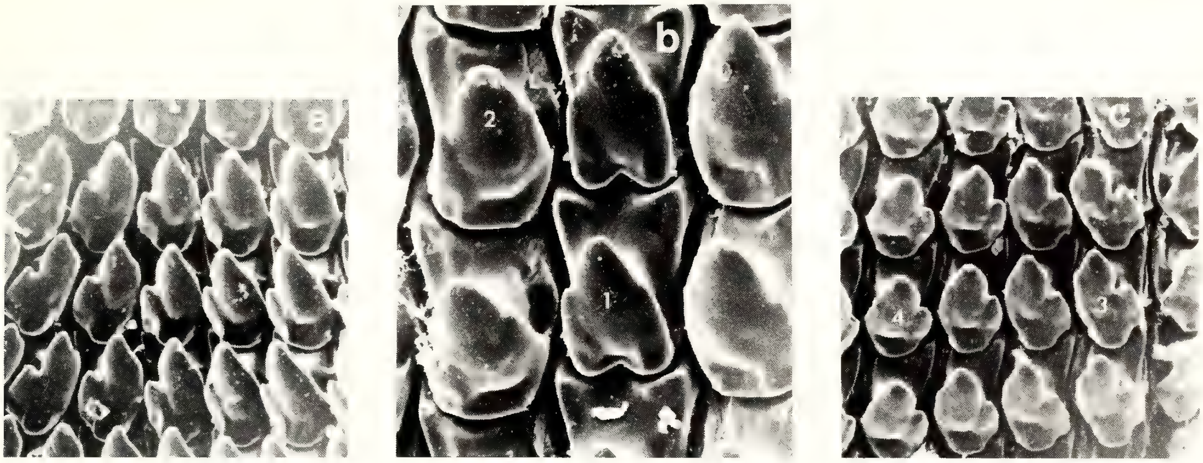

Fig. 3. Radula of *Aegista laoyelingensis*. a, left marginal teeth; b, (1) a central tooth; (2) a left lateral tooth; c, (3) a right marginal tooth; (4) a right lateral tooth.

each lateral tooth, but the inside edge is evenly rounded (Fig. 3b: 2). There is a gradual change in tooth form from the lateral teeth to marginal teeth. The distinction of marginal teeth from the lateral teeth can be described by the following characters: (1) the marginal teeth are longer than the laterals (Fig. 3c, 4), (2) the cusp on the outside edge of each marginal tooth (Figs. 3a and 3c: 3) has a sharper point than each lateral tooth does.

Digestive system. Major features are shown in figure 4: (1) the oesophagus (OE) is distinctly separated from the crop (C); (2) cylindrical crop widens from the oesophagus to the stomach (S); (3) intestinal loop is long, reaching the level of the distal limit of the crop; (4) internal morphology shows 6-7 unciliated ridges run from the upper end of the oesophagus into the stomach.

Reproductive system. The reproductive tract is shown in figure 5. Major features are: (1) two mucous glands (M) connect to an accessory sac (AC) along with the dart sac (DS). There is a sharp, calcified dart (dotted line, Fig. 5, DS), about 1.2-1.3 mm long (Fig. 7); (2) each mucous gland is hollow, and the gland cavity (GC) is surrounded by a thick and wrinkled wall. (Fig. 6: W); (3) flagellum absent; (4) a short epiphallus [Fig. 5: E, (3.4 mm long)] cannot be distinguished from the penis externally, the differences only

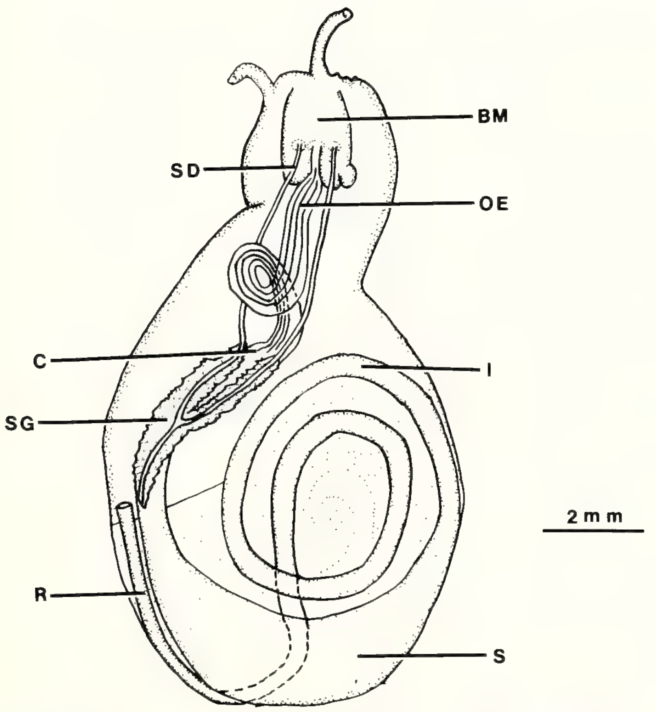

Fig. 4. Digestive tract of *Aegista laoyelingensis*. BM, buccal mass; C, crop; I, intestine; OE, oesophagus; R, rectum; S, stomach; SD, duct of salivary gland; SG, salivary gland.

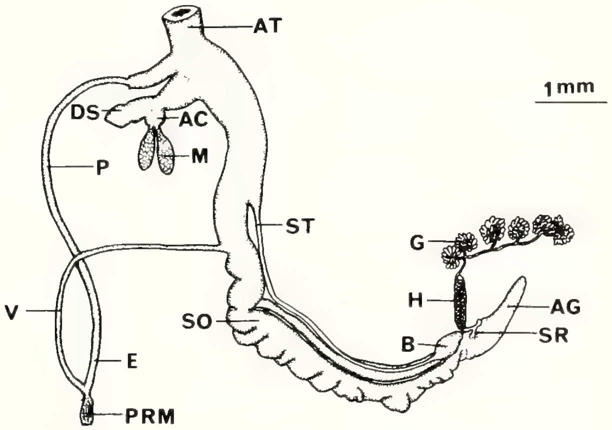

Fig. 5. Reproductive system of *Aegista laoyelingensis*. AC, accessory sac; AG, albumen gland; AT, atrium; B, bursa copulatrix sac; DS, dart sac; E, epiphallus; G, gonad (ovotestis); H, hermaphroditic duct; M, mucous gland; P, penis; PRM, penial retractor muscle; SO, spermoviduct; SR, seminal receptacles; ST, stalk of bursa copulatrix; V, vas deferens.

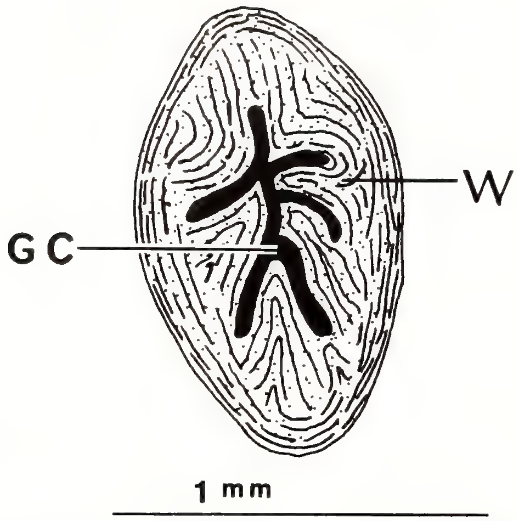

Fig. 6. Cross section of a mucous gland of *Aegista laoyelingensis.* GC, gland cavity; W, wall of the cavity.

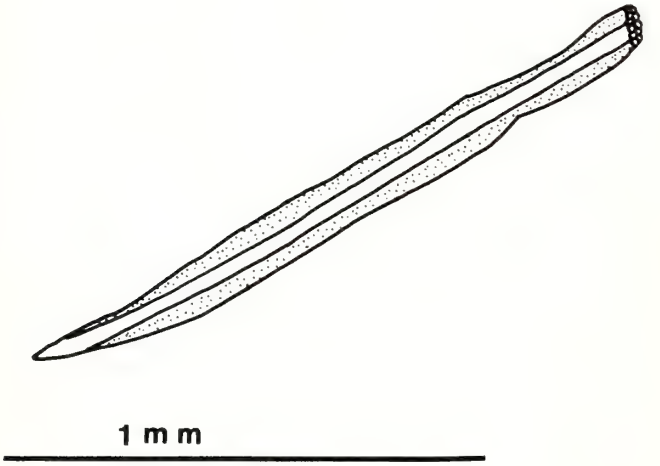

Fig. 7. Dart of *Aegista laoyelingensis.*

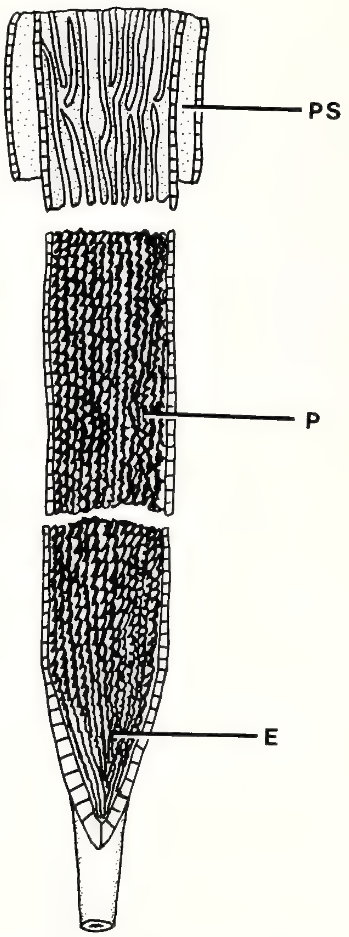

Fig. 8. Internal morphology of the penis. E, epiphallus; P, penis; PS, penis sheath.

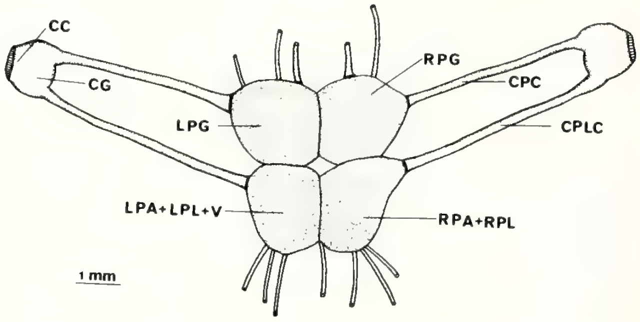

Fig. 9. Central nervous system of *Aegista laoyelingensis.* CC, cerebral commissure; CG, cerebral ganglia; CPC, cerebrol-pedal connective; CPLC, cerebral-pleural connective; LPA+LPL+V, left parietal ganglion and left pleural ganglion plus visceral ganglion completely fused; LPG, left pedal ganglion; RPA+RPL, right parietal and right pleural ganglia fused; RPG, right pedal ganglion.

can be seen by cutting and opening the penial wall; (5) internal morphology of the epiphallus shows 7-8 longitudinal ridges (Fig. 8: E); (6) penis (P) has longitudinal radiating rows of pustules, lower portion of the penis has anastomosing longitudinal ridges, but without verge and penial pilaster (Fig. 8); (7) spermoviduct (SO) length is about 21.8 mm; duct of bursa copulatrix (ST) length is 14.4 mm.

Central nervous system. The central nervous system is shown in Figure 9. The features are: (1) the length of cerebral ganglia (CG) are about 2.0 mm; (2) the length of the cerebral commissure (CC) is about 1.4 mm; (3) the length of the cerebral-pedal connective (CPC) is about 6.1 mm; (4) the length of the cerebral-pleural connective (CPLC) is about 7.6 mm; (5) the right pleural (RPL) and the right parietal ganglia (RPA) are completely fused, the fused ganglion is about 1.6 mm long; (6) the left pleural (LPL) and the left parietal ganglia (LPA) plus the visceral ganglion (V) are completely fused, the fused ganglion is about

1.6 mm long.

Comparisons. I compared *Aegista laoyelingensis* with the published species from China (Table 1) and the collections of *Aegista* at the ANSP, National Museum of Natural History, Washington D. C., and Institute of Zoology of Beijing (Heude Museum) (China). I also compared this species with some more recently described species of *Aegista* from Japan (Kuroda and Habe, 1951; Habe, 1957; Azuma, 1970; Sorita, 1980; Ogaito and Sorita, 1981; Azuma and Azuma, 1982; Sakurai and Sorita, 1982; Minato, 1983; Minato, 1988). I list the following characters to distinguish *Aegista laoyelingensis* from all other known

Table 1. Comparisons among *Aegista laoyelingensis* and the published species from China.

Species (Author)	# of Whorls	Diam. (mm)	Diagnostic characters	Surface	Peristome
Aegista oculus (Pfeiffer)	8	25	Periphery subangular, white banded	Rugosely plicate	Subangulately reflected, white and thin
A. chinensis (Philippi)	8	25	Last whorl slowly increasing	Shining	White, sublabiate
A. vermes (Reeve)	8	32	Last whorl scarcely deflected in front, periphery subangular	Shining, with a white line	Whitish
A. pseudochinensis (Möllendorff)	8	27	Last whorl a little defected	Shining	Reddish widely reflected
A. herpestes (Heude)	7	22	Last whorl obsoletely angulated	Whitish band	White, narrowly reflected
A. furtiva (Heude)	6	19	Last whorl narrow, with obsoletely angulated periphery	Slightly impressed suture	White, expanded
A. aubryana (Heude)	7	21	Periphery obtusely angulated, deflected in front	Brownish white	White and thin
A. accrescens (Heude)	7	16	Last whorl obtusely angulated	With a whitish band	White, narrowly reflected
A. alphonsi (Deshayes)	7	9	Last whorl a little deflected, obtusely angulated above	Irregularly punctate	Thick, sinuous, reflected
A. platyomphala (Möllendorff)	7	17.5	Last whorl obtusely angulated above	Well impressed suture	Thick and white
A. subchinensis (Möllendorff)	7	17	Last whorl scarcely descending in front, sugangulated on the periphery	Shining, with a narrow white band	Thick and white
A. initialis (Heude)	6	12	Last whorl with obtuse white banded peripheral angle	Minutely striate	White, sinuous and thick
A. serpestes (Heude)	7.5	16	Last whorl with obsoletely angulated periphery	Shining	White and thick
A. hupeana (Gredler)	6.5	13-17	Last whorl with angulated periphery	Somewhat shining	Broadly expanded, thick
A. permellita (Heude)	7.5	19	Last whorl keeled	Slightly impressed suture	White
A. tenerrima (Möllendorff)	6	18	Last whorl with subangulated periphery	Slightly impressed sture	White and thick
A. virilis (Gredler)	7	15	Last whorl with obtusely angulated periphery	Shining	Little expanded
A. laurentii (Gredler)	4.5	11	Last whorl large	Shining	Not reflexed
A. radulella (Heude)	6	13	Last whorl with obtusely angulated periphery	Wart-like scales	Acute
A. araneaetela (Heude)	5	9	Last whorl widely umbilicated	Strongly costate	Acute
A. puberosula (Heude)	8	10	Last whorl with obtusely angulated periphery	Minute granulous scales	Little reflected
Plectotropis cathcartae (Reeve)	6	27	Periphery compressly carinated	Reddish corneous	White
P. mackensii (Adams & Reeve)	6.5	30	Periphery acutely carinated	Hairy	Expanded above, thin
P. gerlachi (Möllendorff)	6	19-21	Last whorl with hairy carina	Suture superficial	Simple, a little reflected below
P. laciniosula (Heude)	6	30	Periphery acutely carinate	Hairy	White, slightly expanded
P. trichotropis (Pffeiffer)	6.5	17	Last whorl with acute ciliated periphery	Slightly impressed spiral lines	Simple, a little expanded above
P. mellea (Pffeiffer)	5	22	Periphery carinated	Shining	White, narrowly expanded above
P. tapeina (Benson)	6	15.5	Last whorl descending in front	Thread-like suture	White, dextrally a little expanded
P. hupensis (Gredler)	6.5	20	Last whorl not descending in front, base convex, subangulated, around the umbilicus	Brownish above, whitish-rayed below	White
P. shanghaienwsis (Pffeiffer)	7	13	Last whorl not descending, periphery carinated	Shining	Subreflected, simple
P. barbosella (Heude)	6.5	15	Last whorl obsoletely angulated	Shaggy epidermis	Little thick
P. Diploblepharis (Möllendorf)	5.5	11.5	Last whorl keeled	Shining	White and thick
P. submissa (Deshayes)	4.5	11	Periphery angulated	Smooth	Thick and white

species in the genus:

1. Shells small (diameter = 13.0 ± 1.1 mm) in size for the genus (diameter range for the larger congeners is 15-32).

2. Whorls number 5.5 ± 0.1; last whorl never keeled or angulated, shell surface rough.

3. Flagellum absent (an important character to distinguish the new species from these published species in Japan). Other congeners have either a long or short flagellum (*A. trochula* Adams, 1868; *Aegista kandai* Azuma, 1970; *A. tokyoensis* Sorita, 1980; *A. nunobikiensis* Ogaito and Sorita, 1981; *A. hakusanensis* Azuma and Azuma, 1982; *A. itoi* Kuroda and Azuma, 1982; *A. kanmuriyamensis* Azuma and Azuma, 1982; *A. tokyoensis choshiensis* Sakurai and Sorita, 1982; *A. tadai* Minato, 1983).

The shell of *Aegista laoyelingensis* most closely resembles in shape that of *A. furtiva* Heude, 1885, from Southwestern China; but the latter shell is larger (diameter, 19 mm), the surface smoother, the peristome white, thicker and more widely reflected, and the last whorl has an obsoletely angulated periphery.

DISCUSSION

Minato (1988) listed more than 70 species and subspecies of *Aegista* from Japan and nearby islands. Kuroda and Habe (1951) placed the genus *Aegista* in the subfamily Aegistinae, based on different characters of shells and genital organs (such as, snails with more or less strongly developed flagellum). Their classification follows (see Habe, 1955):

Family: Bradybaenidae
  Subfamily: Aegistinae
    Genus: *Aegista* Albers, 1850
      Subgenera:

Aegista Albers, 1850. Type species: *Aegista chinensis* (Philippi, 1845).

Plectotropis Martens, 1860. Type species: *Plectotropis elegantissima* (Pfeiffer, 1849).

Coelorous Pilsbry, 1900 (in *Coccoglypta* Pilsbry 1900, see Richardson, 1983). Type species: *Coccoglypta cavicollis* (Pilsbry, 1900).

Buliminopsis Heude, 1890 (in *Pseudobuliminus* Gredler, 1886, see Richardson, 1983). Type species: *Pseudobuliminus buliminoides* (Heude, 1882).

Trishoplita Jacobi, 1898 (placed in Bradybaeninae, see Richardson, 1983). Type species: *Trishoplita pallens* (Jacobi, 1898).

Nesiohelix Kuroda and Emura, 1943 (placed in Bradybaeninae, see Richardson, 1983). Type species: *Nesiohelix caspari* (Möllendorff, 1884).

Bradybaenid shells are variable in form (ranging from globose to depressed or lens-shaped), and in color pattern (from uniformity to many banded). For this reason Pilsbry (1895) listed some anatomical characters (but in his paper, the external anatomy and genitalia for *Aegista* were unknown) for distinguishing different genera of the Bradybaenidae. He concluded that *Plectotropis, Mastigeulota* and *Euhadra* possess a flagellum. The other genera lack it, probably by degeneration. It is likely that the degeneration had occurred in some Asian species grouped in *Aegista* too, such as the species reported by Wiegmann (1900): *Plectotropis diploblepharis* Möllendorf, 1902; *P. submissa* Deshayes, and *Aegista laoyelingensis*. The flagellum of these species is almost always lacking. Accordingly, it appears that the classification of the Aegistinae by Kuroda and Habe cannot be accepted prior to a complete revision in *Aegista*.

I agree with Nordsieck (1987) that the Asian Bradybaenidae (with stimulatory organ consisting of a dart sac, usually with an accessory dart sac and one or two dart glands) represent (in contrast to the American or the European Helicoidea) a strikingly consistent group, that cannot be arranged into subfamilies. For the Bradybaeninae species (distributed in Eastern Asia), they have the stimulatory organ with two dart glands that are usually divided. Since the different groups from Japan do not differ in the structure of the stimulatory organ (see Azuma, 1970; Sorita, 1980; Ogaito and Sorita, 1981; Azuma and Azuma, 1982; Kuroda and Azuma, 1982; Sakura and Sorita, 1982; Minato, 1983), there is no reason to divide Bradybaeninae into more subfamilies. Only the groups distributed in the Philippines can be separated based on the structure of its stimulatory organ (stimulatory organ with one simple dart gland), as the subfamily Helicostylinae.

Mantle pigment patterns are variable in *Aegista laoyelingensis*. Cain (1971) gave a detailed description of mantle polymorphisms in *Monacha cantiana* (Montagu) and demonstrated that mantle color is genetically controlled. Because the specimens used in my research were collected from a population in a habitat with the same environmental factors (temperatures and vegetation), the variation of mantle pigmentation could be caused by genetic mutations.

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Annual gonadal cycle of the land snail *Scutalus tupacii* (Pulmonata: Bulimulidae)

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Abstract: The annual gonadal cycle and its relation to the seasons were investigated in the land snail *Scutalus tupacii* (d'Orbigny). Collections of adult snails were carried out monthly over two consecutive years. The animals were processed for anatomical and histological studies. The ovotestis is composed of a number of tubules or elongated acini, each one containing both male and female sexual cells as well as Sertoli and follicular cells. Spermatogenesis and oogenesis occur in all the acini.

The annual cycle of the ovotestis was divided into three phases: 1) Pre-breeding (September-November: Spring), characterized by the reactivation of spermiogenesis and the subsequent increase in number of mature sperm; 2) Breeding (November-February: Spring-Summer), characterized by the great number of spermatozoa in the gonad, and the highest proportions of mature oocytes; 3) Post Breeding (March -September: Autumn-Winter, with abundance of spermatogonia, oogonia and primary spermatocytes, and the interruption of spermiogenesis.

Although the proliferation of male and female germinal cells is practically coincident, male gametes attained maturity at least one month before the female gametes. The post-breeding period occurs during hibernation which is coincident with the dry season. Based on the data obtained, the annual cycle of reproductive activity in this species depends principally upon the wet or rainy season.

The annual gonadal cycle of many species has been previously investigated [e.g. *Lymnaea stagnalis* (Linné) (Berrie, 1966); *Helix pomatia* (Lind, 1973); *Semperula maculata* (Tompleton) (Nanaware and Varute, 1975); *Helix aspersa* Müller (Gomot and Griffond, 1987)]. Related works include research on the maturation of the reproductive tract of various species (see Lusis, 1966; Smith, 1966; Runham and Laryea, 1968; Sokolove and McCrone, 1978; Runham and Hogg, 1979; Cuezzo, 1990) as well as the life cycles of a number of groups (see Van Der Laan, 1975, 1980; Hodasi, 1979; Bailey, 1980; Solem, 1984; Roth, 1986). More recently, there have been a growing number of studies that analyse the influence of different factors on gametogenesis under laboratory conditions (Gomot and Gomot, 1988; Gomot, Gomot and Griffond, 1989; Griffond and Medina, 1989).

The genus *Scutalus* Albers, 1850, is well represented in the western region of Tucumán Province (27°S, 66°W), Argentina. Despite the large and widespread populations, very few data are available regarding the biology of these bulimulid land snails. In the hope of filling part of this gap, a population of *S. tupacii* (d'Orbigny) was sampled over two consecutive years to find out the characteristics of the gonadal cycle and the possible changes that occur during the different seasons.

MATERIALS AND METHODS

Monthly collections of adult land snails *Scutalus tupacii* were carried out from September 1988 to March 1991 in "Reserva Aguas Chiquitas" (El Cadillal, Tucumán, Argentina), which is part of the subtropical tucuman-bolivian forest. The samples were divided into two groups. One group used for histological studies was fixed in Bouin's or in Baker's fixative (Humanson, 1979). A second group was used for anatomical analysis, after being relaxed in cooled boiled water. These were then immersed in Baker's fixative. The ovotestis and hermaphroditic duct were dissected out, dehydrated in an ascending alcohol series, embedded in Paraplast and sectioned at 6 μm. Sections were stained with Ehrlich haematoxylin-eosin and Mallory (Azan) Heidenhain (Humanson, 1979).

Monthly, ovotestis and hermaphroditic ducts were fixed in Karnovsky's solution (Karnovsky, 1965) with 0.1 M phosphate buffer (pH 7.2), post-fixed in 2% osmium tetroxide and embedded in Epon-araldite. Semi-thin sections of 1 μm were stained with toluidine blue and examined by light microscope. Voucher specimens have been deposited in the Fundación Miguel Lillo's malacological collection (Catalogue No. FML 001000).

RESULTS

As in other pulmonate gastropods, the ovotestis or hermaphroditic gonad of adult *Scutalus tupacii* is found embedded in the digestive gland which is located in the upper whorls of the shell. The activity and the size of the ovotestis depend upon the age and size of the animal as well as the season. The structure of the ovotestis was found to be similar to most pulmonates (Joosse and Reitz, 1969; Luchtel, 1972a, b; de Jong-Brink *et al.*, 1977).

From November to May (end of Spring to early Autumn), the acini are whitish and clearly separated from each other. At the beginning of April, a progressive reduction in the size of the ovotestis occurs that peaks between June and July (Winter). The decrease in length and diameter of the acini are accompanied by a change in colouration from white to light brown. The pigmentation is more evident in the distal part of the acini. In October the ovotestis progressively begins to recover its size and color.

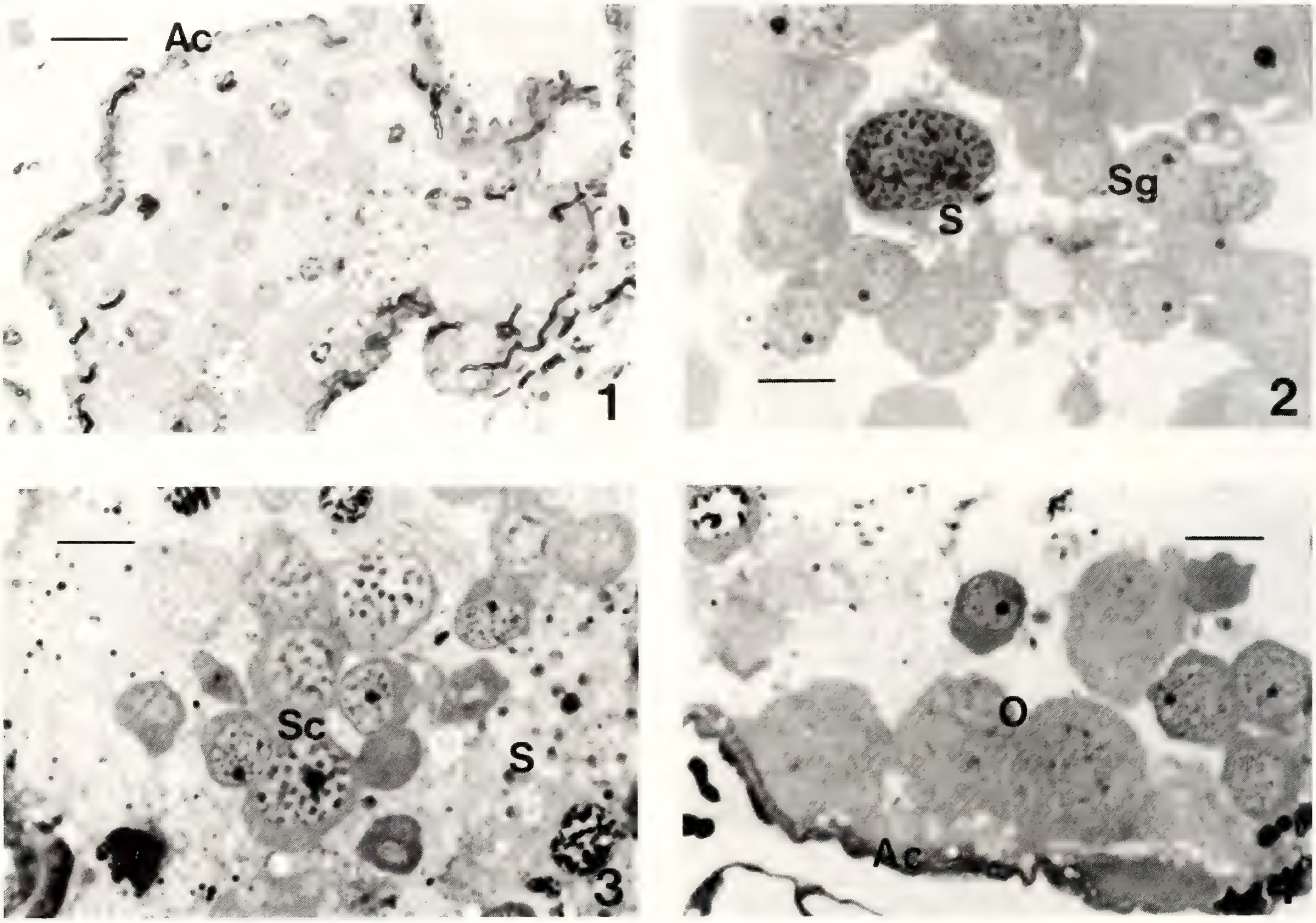
The annual cycle of the ovotestis can be divided into three phases of activity: 1) Post-breeding phase (March-September), Fall-Winter; 2) Pre-breeding phase (September-October), Spring; 3) Breeding phase (November-February), Spring-Summer.

1) Post-breeding phase (Figs. 1-4):

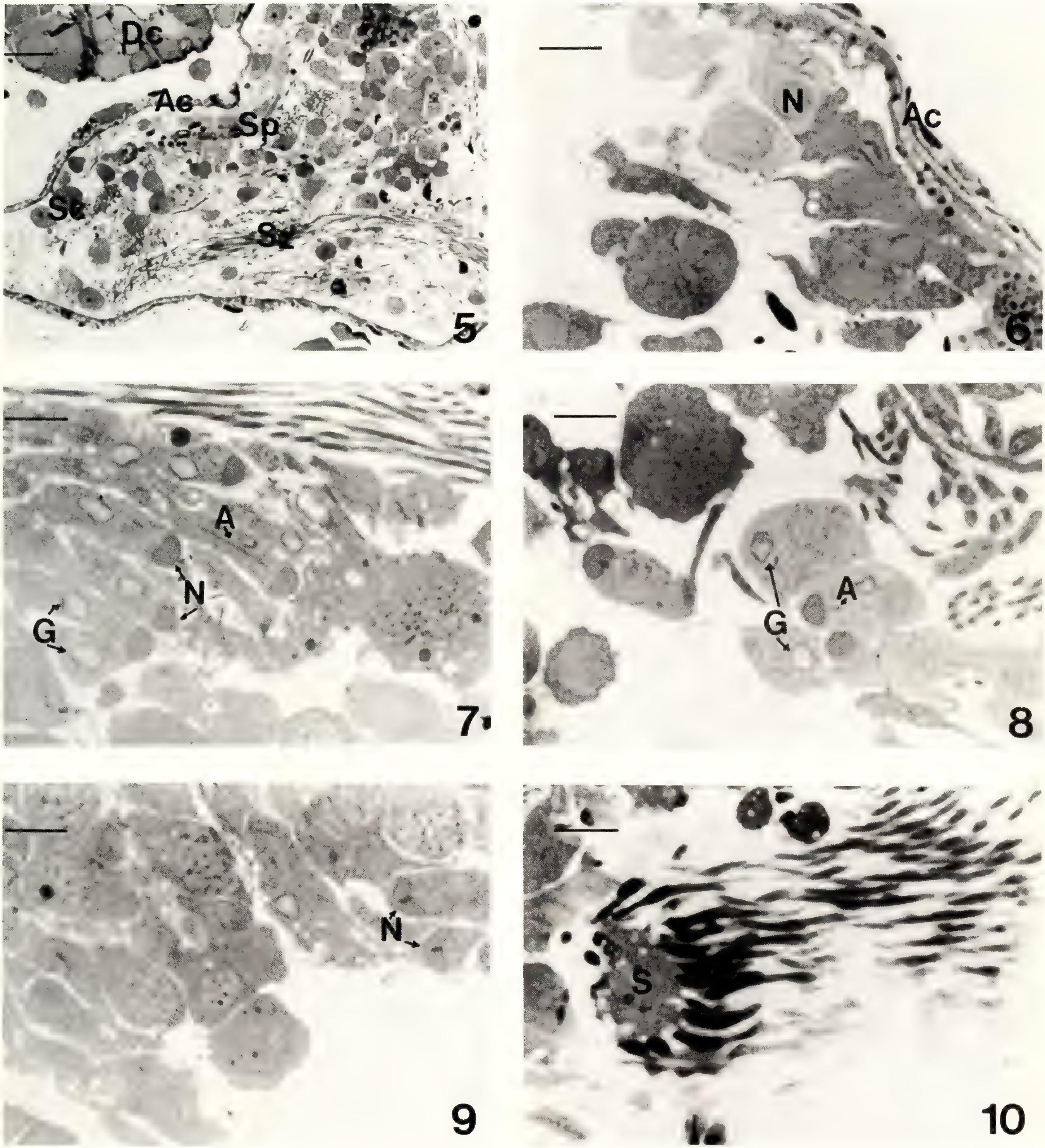
During this phase the acini are small in diameter with abundant interacinar space (Fig. 1). The post-breeding part of the cycle is characterized by an abundance of spermatogonia and primary spermatocyte (Figs. 2, 3). Oogonia are present isolated or in clusters of two to four cells and are always located inside the epithelium lining the acini, remaining in contact with the basal lamina. These cells are recognizable by a poorly contrasted cytoplasm (Fig. 4). Spermatids are scarce and are present only in early stages of differentiation. Few morphologically mature spermatozoa are present in the lumen of the acini. In the distal region of the acini the presence of mature Sertoli cells is remarkable. Their abundant cytoplasm is highly vacuolated and extends into the lumen, contributing to the "packed' appearance of the acini. Male germ cells at different stages of differentiation are clearly embedded within the same Sertoli cell.

2) Pre-breeding period (Figs. 5-10):

Externally the ovotestis maintains the same appearance as in winter. The acini have few or lack spermatozoa



Figs. 1-4: Post-breeding period. **Fig. 1.** General appearance of the acini during the Post-breeding period (Ac, acinar wall; scale bar = 20 μm). **Fig. 2.** Group of spermatogonia (Sg) in close contact with a Sertoli cell (S) with dark nuclei (scale bar = 10 μm). **Fig. 3.** Group of spermatocytes (Sc) embedded in the cytoplasm of a Sertoli cell (S). (scale bar = 10 μm). **Fig. 4.** Three young oocytes in contact with the acinar wall (O, oocyte; Ac; acinar wall, scale bar = 10 μm).



Figs. 5-10: Pre-breeding period. **Fig. 5.** General aspect of an acinus during the pre-breeding period (Ac, acinar wall; Sc, spermatocytes; Sz, spermatozoa; Sp, spermatids; S, Sertoli cells; scale bar = 40 μm). **Figs. 6-9.** Different stages of spermatid maturation. **Fig. 6.** Early spermatid stage. These cells possess a round nucleus with anterior and posterior plaque already differentiated (N, nucleus; scale bar = 10 μm). **Figs. 7-9.** Mid spermatid stage. The nucleus becomes indented at the posterior plaque. An elongating axonome is visible. (N, nucleus; A. axoneme; G, Golgi apparatus; scale bar = 10 μm). **Fig. 10.** Late spermatid stage. Elongated nucleus with condensed chromatin. The heads are embedded in the cytoplasm of a Sertoli cell (S). (scale bar = 10 μm).

(Fig. 5). Toward the end of September and the beginning of October spermatids proliferate and different stages start to become apparent (Figs. 6-10). Spermatids become more abundant than spermatocytes. Also a growing number of spermatozoa can be observed in the lumen of the acinus. At the bottom of the acini vitellogenic oocytes are present but never more than one per acinus.

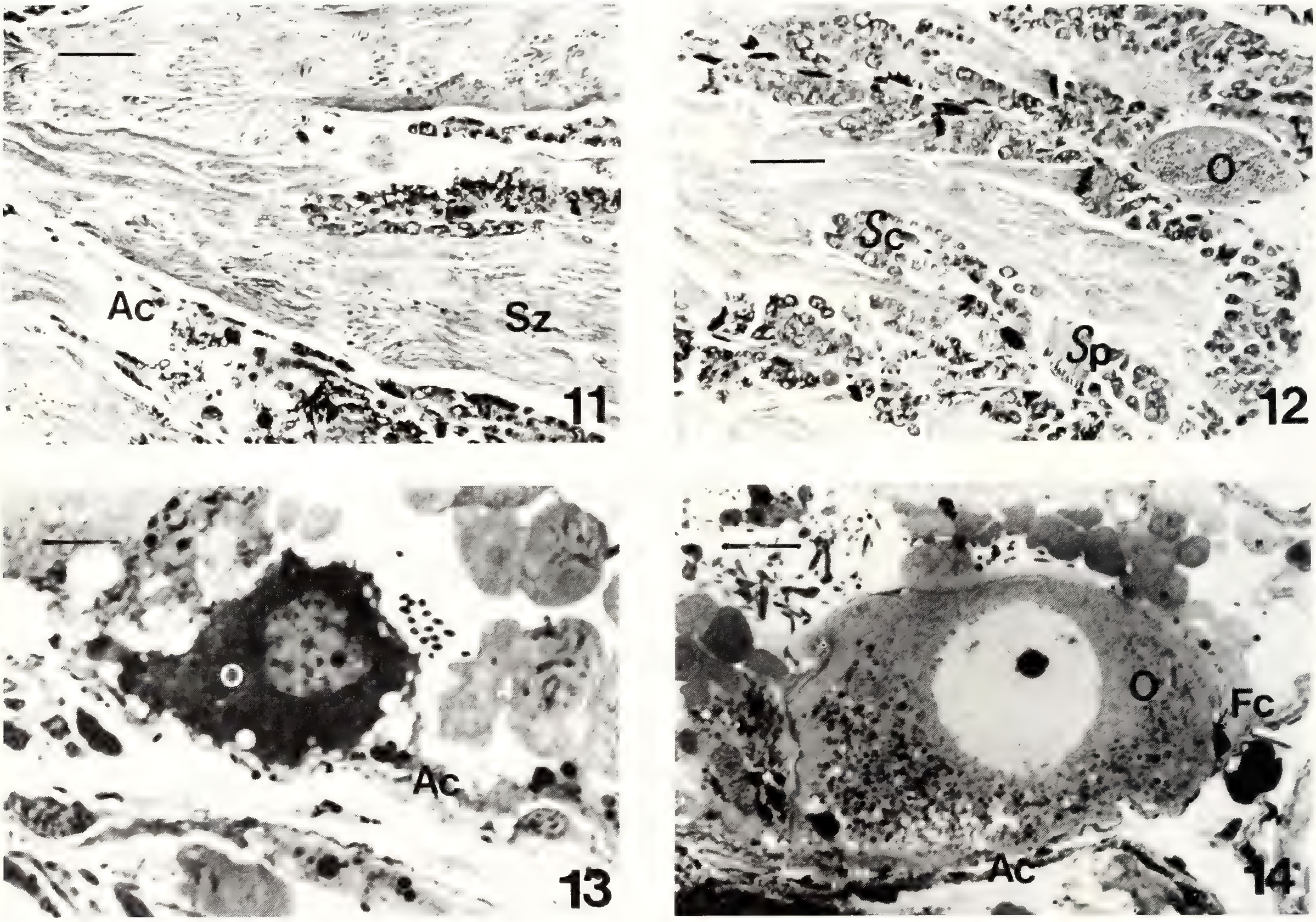
3) Breeding period (Figs. 11-14):

During this part of the cycle all the spermatogenic stages, from spermatogonia to spermatozoa are present in the ovotestis (Figs. 11, 12). The lumen of the acini are filled with spermatozoa. Concerning the female line, previtellogenic and vitellogenic oocytes (Figs. 13, 14) (Griffond and Bolzoni-Sungur, 1986) are distributed along the acini with a tendency towards maturation near the bottom of the acinus.

In longitudinal sections of ovotestis (Figs. 11, 12), no interacinar space is observed and the layers of the adjacent acini are in contact. The ovotestis of individuals that had just copulated were almost empty, lacking mature male gametes.

The male phase in the ovotestis of *Scutalus tupacii* starts during the post-breeding period with an active proliferation of spermatogonia and spermatocytes, coincident with hibernation (end of autumn and during winter). Although mature spermatozoa are present in the ovotestis in every month of the year it is important to remark that spermiogenesis is inactive during winter. Therefore the mature gametes are less abundant in the acini while the snails are hibernating. As soon as spermiogenesis begins, toward the end of October and beginning of November, the lumen of the acini fills with spermatozoa.

Mature oocytes are present throughout the year being especially abundant during the breeding period.



Figs. 11-14: Breeding-period. **Fig. 11.** Longitudinal section of the proximal part of several acini. The lumens are saturated with spermatozoa (Sz) (Ac, acinar wall; scale bar = 40 µm). **Fig. 12.** Longitudinal section of the distal portion of several acini. The more advanced stages, spermatocytes (Sc), spermatids (Sp) and mature oocytes (O) are observed in this region (scale bar - 50 µm). **Fig. 13.** Young premeiotic oocyte resting on the acinar wall (Ac) (O, oocyte; scale bar = 10 µm). **Fig. 14.** Vitellogenic oocyte. Note the presence of follicular cells (Fc) that envelope the oocyte (O, oocyte; Ac, acinar wall; scale bar = 20 µm).

Female cell proliferation begins in autumn, during May and June, but the number of mature oocytes grow between November and December in the pre-breeding and breeding periods.

The seminal vesicle stores spermatozoa throughout the year. In the summer months, however, a noticeable increase in both the number of stored male gametes and the diameter of the hermaphroditic duct was noted. Although rather constant patterns were recorded in the three reproductive periods, individual variation in the lengths of the periods existed.

SEASONALITY IN THE REPRODUCTION

According to W. Koppen's climatic classification (Torres Bruchman, 1976), the region that this population inhabits has a mesothermal climate with a dry winter (temperature of the warmest month higher than 22°C and of the coldest month lower than 18°C). The vegetation corresponds to a basal subtropical forest which is characterized by the presence of big trees [*Phoebe porphyria* (Grisebach) Mez, *Jacaranda mimosifolia* D. Don, *Juglans australis* Grisebach and *Tipuana tipu* (Benth.) O. Kuntze] associated with epiphyt plants like *Phlebodium aureum* (L.). Abundant ferns with wide front fronds cover the ground. The presence of a wet season in the region is the key to understand the pattern of activity of these land snails. The length of this period is approximately 6 months with the heaviest rains between January and March (Fig. 15). Winter is the dry season when the snails are most of the time dormant. In1989, the dry season was longer than in 1990 and consequently the hibernation period was prolonged. At the beginning of the dry period most of the animals bury themselves vertically with the aperture of the body whorl below the soil and the spire above. Other snails simply protect themselves under a thick layer of dry leaves and secrete a thin, transparent epiphragm. No mucus tracks were observed during these months (temperature range: 0 - 20°C). Another noticeable change is the retraction of the animal's body into the shell as a consequence of weight and water loss.

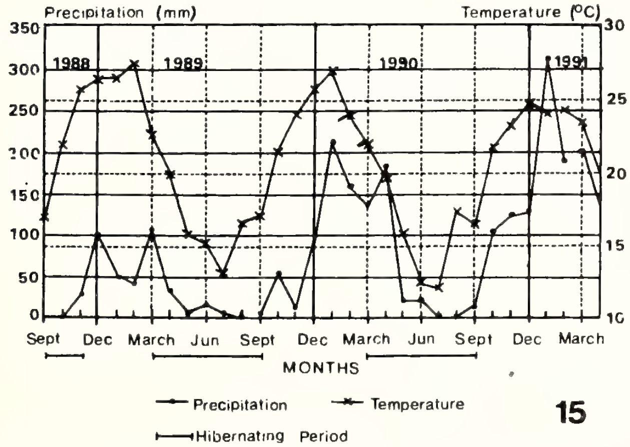


Fig. 15. Dry and wet seasons from 1989 to 1991.

Reproductive activity begins between October and November when the first rains can deeply moisten the soil. From this moment it is possible to observe copulating snails, especially nocturnally, but also during certain days, in particular the rainy ones. Mating can last several hours. The first clutch of eggs, both in 1988 and 1989, were found in November, generally buried in moist soil at the base of large trees. The eggs have an opaque-white albuminous substance within a nearly transparent membrane. The number of eggs per clutch ranged from 70 to 120 with diameters from 2.5 to 3.0 mm. Under laboratory conditions the duration of development ranged from 15 to 18 days.

DISCUSSION

Three different regions in gonadal acini of *Helix aspersa* juveniles (Griffond and Bride, 1987) and in *Biomphalaria glabrata* (Say) (de Jong Brink, 1976) have been described. In adult *Scutalus tupacii* these regions are not clearly identifiable. A trend toward a compartmentalization in male medullar and female cortical regions occurs. Also there is a higher frequency of vitellogenic oocytes, mature follicular and Sertoli cells at the bottom of the acinus. Morphologically mature spermatozoa are found in the acinar lumen with their nuclei oriented toward the bottom and the flagellae toward the neck of the acinus.

Despite the lack of strict regionalization, most of the mature gametes are typically found at the bottom of each acinus. Young germinal cells are distributed randomly along the acini. Coincidently, Runham and Hogg (1979) have found in *Deroceras reticulatus* (Müller) that there is a gradient of oocyte size being largest at the acinar base. However, they also noted that the great enlargement of the acini could, by itself, completely explain the observed oocyte distribution: largest oocytes arise first from the base, the oldest part of the acinus and remain there without any active movement.

Although proliferation of male and female germinal cells is practically coincident, male gametes reach maturity at least one month before the female ones. A number of studies, carried out in several species (Lusis, 1966; Runham and Laryea, 1968; Luchtel, 1972; Runham, 1978) support the hypothesis of a clear separation in time of male and female phases without superposition in the time of proliferation of the germinal cells. During the breeding period of *Scutalus tupacii* both mature spermatozoa and oocytes are present in the ovotestis, coincidently with the summer months and wet season. During winter, the dry season, hibernation takes place and gonadal activity is minimal with predominating male and female juvenile germinal cells.

Luchtel (1972) suggests that *Arion circumscriptus* L. would be defined as a protandrous hermaphrodite considering the time at which the male and female gametes reach maturity. However, in terms of time of differentiation of the spermatogonia and oogonia the species could be considered a simultaneous hermaphrodite and finally in terms of appearance of primary spermatocytes and oocytes *Arion* could be a protogynous hermaphrodite.

Scutalus tupacii could be considered a protandrous hermaphrodite if we define "protandry" as the maturation of male gametes earlier than the female. However the presence of mature oocytes and spermatozoa is coincident during the breeding period without a great separation in time of both phases. Among the pulmonates already studied, most are true protandric hermaphrodites (Lusis, 1966; Smith, 1966; Runham and Hunter, 1970; Parivar, 1978) except for the Achatinellidae which are registered as protogynous.

Based upon the analysis of the climatic data (Fig. 15) and mainly upon observations in the field, the annual cycle of activity in *Scutalus tupacii* depends principally upon precipitation. With the beginning of the wet season in the summer the snails start their reproductive activity, copulating and laying eggs during these months. The duration of hibernation is intimately related to the duration of the dry season. The other factors such as the temperature and photoperiod, are not as important as precipitation and humidity of the habitat in the actvitity cycle of *S. tupacii.*

ACKNOWLEDGMENTS

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Functional anatomy of *Fossula fossiculifera* (D'Orbigny, 1843) (Bivalvia: Mycetopodidae)

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Abstract: *Fossula fossiculifera* (D'Orbigny, 1843) is the type species of the genus *Fossula*, a member of the family Mycetopodidae. The genus is restricted to South America. The species is found in the Paraná River and its tributaries from Argentina to the state of São Paulo, Brazil, and in the Paraguaçu River on the Atlantic ridge of the state of Bahia, Brazil. These medium-sized bivalve molluscs live buried in muddy substrata. The incurrent aperture is fringed along the inner fold while the excurrent aperture is smooth. The ctenidia are of type D (Atkins, 1937a). The stomach is a type IV structure (Purchon, 1958) with morphological differences on the right wall. The posterior gut is voluminous; the typhlosole runs throughout its length. The animals are hermaphrodites and incubate their eggs in the marsupium of the inner demibranchs.

In South America the family Mycetopodidae is represented by six genera: *Fossula, Iheringella, Monocondylaea, Leila, Anodontites,* and *Mycetopoda* (Parodiz and Bonetto, 1963). According to Ortmann (1921), *F. fossiculifera* (D'Orbigny, 1843) occurs in the Paraná River and its tributaries from Argentina to the state of São Paulo, Brazil. Bonetto (1961), when discussing the geographic distribution of unionoideans in the Argentine Republic, extended the distribution of *F. fossiculifera* to the Paraguaçu River, on the Atlantic ridge of the state of Bahia, Brazil.

Hass (1930) recognized three subspecies of *Fossula: F. fossiculifera fossiculifera, F. fossiculifera balzani* (Ihering, 1893), and *F. fossiculifera braziliensis* (Ihering, 1910). According to this author, *F. fossiculifera fossiculifera* is distributed as described by Ortmann (1921), whereas *F. fossiculifera balzani* occurs in the Paraguai River, state of Mato Grosso do Sul, Brazil, and *F. Fossiculifera braziliensis* occurs in the Paraguaçu River, state of Bahia, Brazil. Ortmann (1921) and Bonetto (1961) recorded a single species for the genus. Lange de Morretes (1949) reported two species, *F. fossiculifera* and *F. braziliensis*, without mentioning the species reported by Hass (1930).

In the present report, I shall follow the systematic treatment proposed by Bonetto (1961). Systematic studies on the functional anatomy of limnic bivalves in Brazil, include those conducted by Mansur (1972, 1973), Hebling and Penteado (1974), Hebling (1976), Veitenheimer and Mansur (1978), Mansur and Anflor (1981), Mansur and Silva (1990) and Avelar and Santos (1991). Additional studies of the functional anatomy of the Mycetopodidae have been reported by Hebling (1976), who studied the comparative anatomy of *Anodontites trapesialis* (Lamarck, 1819) and *A. trapezeus* (Spix, 1827). Mansur (1974) examined the shell and the morphology of the digestive system of *Monocondylaea minuana* (D'Orbigny, 1835). Mansur and Silva (1990) studied the comparative morphology and microanatomy of *Bartlettia stefanensis* (Moricand, 1856) and *A. tenebricosus* (Lea, 1834). Veitenheimer and Mansur (1978) studied the morphology, histology and ecology of *Mycetopoda legumen* (Ortmann, 1888).

The objective of the present investigation was to study the structure, ciliary feeding currents and other functional adaptations of *Fossula fossiculifera* as a contribution to the understanding of the biology of the species, and also to provide the basis for future research related to South American unionideans.

MATERIALS AND METHODS

Live specimens of *Fossula fossiculifera* specimens were collected from the Pardo River, municipality of Ribeirão Preto (21° 7'S, 47° 45'W). Five specimens were captured at three-month intervals (15 Feb, 15 May, 17 Aug and 21 Nov). A total of 20 animals were kept alive in the laboratory in aquaria at 25°C. Some animals were anesthetized with magnesium chloride and fixed in 10% buffered formalin for 24 hr. Others were preserved in 70% alcohol for morphological examination.

To complete the anatomical studies, detailed drawings of the animals, and of the arrangements of their internal organs, were performed using anesthetized animals. Ciliary currents of the mantle, ctenidia, labial palps and stomach were observed under a stereomicroscope using carmine or carborundum as indicators. Some structures (palps, ctenidia, mantle and visceral mass) were fixed in aqueous Bouin's, cut into 7-10 μm sections, and stained with Ehrlich's hematoxylin and eosin, for anatomical examination.

HABITAT

According to Bonetto (1961), *Fossula fossiculifera* occurs in the Paraguai River and in the middle and upper Paraná River, reaching the Atlantic coast of the state of Bahia in the Paraguaçu river. The animals preferentially live buried in muddy substrata under calm waters and can be captured at depths of 0.7 to 1.0 m. The bivalves burrow almost completely into the substratum, leaving only their posterior end exposed (Fig. 1). They can be captured by probing the river bottom with one's hands or feet. Several species of bivalve were captured at the collection site, among them *Anodontites trapesialis, Diplodon rotundus gratus* (Wagner, 1827), *D. fontaineanus* (D'Orbigny, 1835), *D. delodontus expansus* (Küster, 1856), *D. martensis* (Ihering, 1892), and *Castalia undosa undosa* (Martens, 1827). The most abundant species were *D. rotundus gratus* and *A. trapesialis,* followed by *D. fontaineanus* and *F. fossiculifera,* with the rare occurrence of *D. delodontus expansus* and *D. martensi.*

It should be pointed out that bivalves of the families Hyriidae or Mycetopodidae, except *Anodontites trapesialis,* that occur in the Pardo River measuring less than 2 cm in length are difficult to identify because the juvenile shells are very similar and all characterized by the presence of six to 12 ribs in the umbonal region.

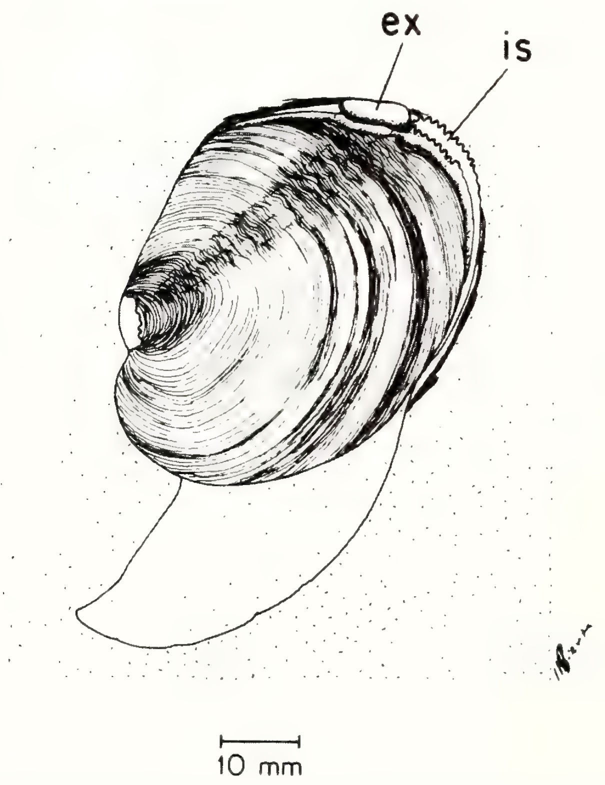

Fig. 1. *Fossula fossiculifera.* External view of the left side showing extended foot and aperture (ex, excurrent aperture; is, incurrent aperture).

FUNCTIONAL MORPHOLOGY

SHELL. The shell of *Fossula fossiculifera* (Figs. 2 and 3) is subcircular in contour, equivalve and inequilateral, with a winged posterior border rising above the umbo. The periostracum in species smaller than 2.0 cm is yellowish to olive-brown in color in specimens ranging in size from 2.0 to 7.0 cm in length. In specimens larger than 7.0 cm, the periostracum is brownish green. These observations are similar to those reported by Ihering (1910) and Ortmann (1921).

The umbo (u) is prosogyrate, with a worn periostracum. The lunule (lu) is small, dark in color and with oval contours. The outer opisthodetic ligament (l) starts below the umbo and extends posterodorsally to the valve isthmus. Two minor ribs originate in the umbo and extend to the ventral region, the most dorsal one ending in the region of the diaphragm that separates the apertures. In young and adult specimens, the growth lines anastomose, especially in the posterior region where they are elevated and have a lamellar aspect. The above observations are sim-

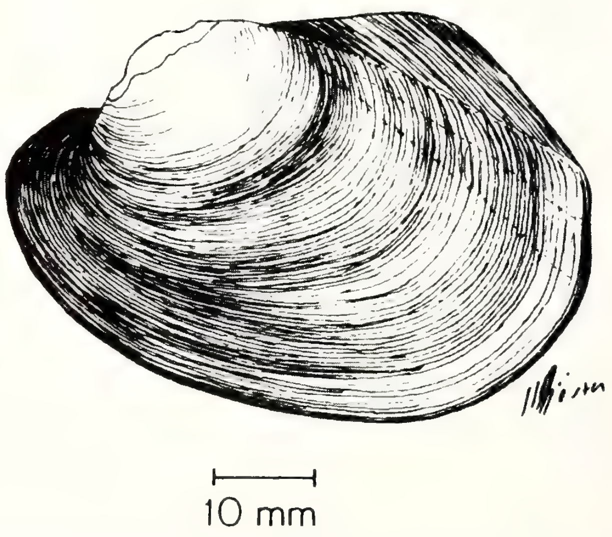

Fig. 2. *Fossula fossiculifera.* External view of the left valve showing the lines of growth.

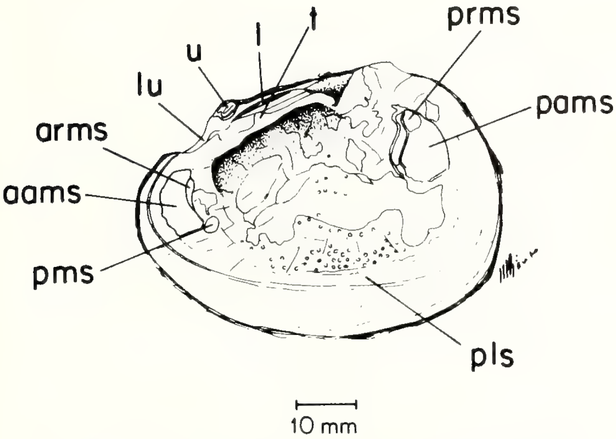

Fig. 3. *Fossula fossiculifera.* Internal view of the right valve, showing the muscle scar (aams, anterior adductor muscle scar; arms, anterior retractor muscle scar; l, ligament; lu, lunule; pams, protractor muscle scar; prms, posterior retractor muscle scar; t, tooth; u, umbo.

ilar to those reported by Hebling (1976) for *Anodontites trapezeus*. According to Ortmann (1921), the valve measurements of *Fossula fossiculifera* varied from 80 to 85%, in relation to length. In the present study, height was 76 to 84% of length in a lot of 20 animals.

The hinge is well developed, with one pseudocardinal tooth in the left valve and two pseudocardinal teeth in the right valve. In specimens larger than 7.0 cm, the spacing between the pseudocardinal teeth in the right and left valves becomes increasingly wider and the teeth simply become a projection of the hinge, eventually even becoming obsolete. The inner surface of the valve is white or bluish white, with the submarginal region yellowish cream in color. In recently sacrificed specimens with soft parts removed, the inner surface stains greenish in color. This results from pallial mucus that polymerizes when in contact with the external medium, and forms a thin film. After a few weeks, this film detaches from the shell revealing the white pearly color of the nacre.

The umbonal cavity is shallow and the scars of the dorsal mantle muscles were not observed. Hebling (1976) reported the presenceof these muscles in *Anodontites trapesialis* and their absence in *A. trapezeus*. The scars of the anterior adductor muscle (aams) and of the anterior retractor muscle of the foot (arms) (Fig. 3) are continuous and present an oval contour. The anterior retractor muscle of the foot forms a deep scar in a position dorsal to the anterior adductor muscle. The scar of the protractor muscle of the foot (pms) has a rounded contour and is located in the region of the posterolateral third of the anterior adductor muscle. The scar of the posterior retractor muscle of the foot (prms) is narrow and dorsally located in relation to the scar of the posterior adductor muscle. The scar of the posterior adductor muscle (prms) is approximately of the same size and shape as that of the anterior adductor muscle. In specimens measuring 40 and 80 mm in length, the size of the scars reached six and 12 mm, respectively.

The pallial line (pls) starts below the scar of the anterior adductor muscle and continues parallel to the margin of the shell, ending at the base of the posterior adductor muscle scar. The margin of the mantle leaves a well defined scar that starts dorsally to the anterior adductor muscle and runs along the entire margin of the shell parallel to the scar of the pallial line and ending dorsally in the shell isthmus.

MANTLE. When the valve and mantle are removed from the left side of the animals, the pallial cavity is exposed. The outer (secretory) and median (sensory) folds of the mantle are quite close to each other. In the region of the incurrent aperture, the inner fold (muscular) has a fringed border appearing to be formed by small papillae, as defined by Ortmann (1921), that extend far forward, decreasing in size and gradually disappearing.

Posterior to the foot, approximately 1 cm dorsad from the shell margin, the mantle presents a muscular elevation forming an evagination that I term the posterior fold of the mantle (pfm) (Fig. 4 and elsewhere) and which ends at the point where the ctenidia join the mantle. Anterior to this fold, the mantle is not thickened, as shown in figure 5.

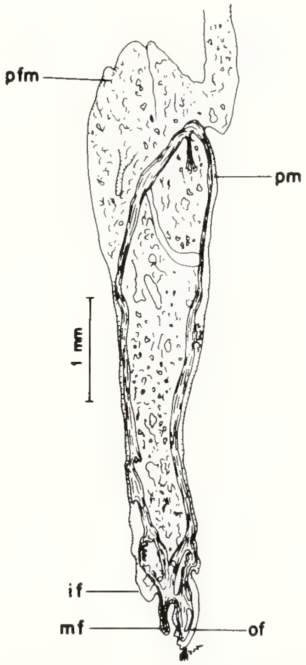

Fig. 4. *Fossula fossiculifera.* Frontal section of the posterior region of the edge of mantle showing the posterior fold of mantle and the pallial muscle on the mantle lobes (if, inner fold; mf, middle fold; of, outer fold; pm, pallial muscle; pfm, posterior fold of mantle).

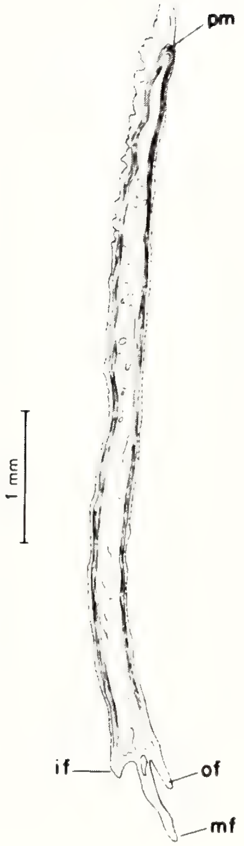

Fig. 5. *Fossula fossiculifera.* Frontal section of the anterior region of the edge of mantle and the pallial muscle (if, inner fold; mf, middle fold; of, outer fold; pm, pallial muscle).

The mantle margin on both the left and right sides presents two joining regions located dorsoventrally to the anal opening, defining the excurrent aperture. The incurrent aperture is characterized by the presence of fringes of the inner margin of the mantle. The mantle is yellowish in color, and the color of the inner, middle and outer lobes tends to be salmon. Between the inner and middle lobes, in the posterior region, there is black pigmentation that delimits the incurrent and excurrent apertures. The pedal opening is wide and starts in the region located posteroventrally to the anterior adductor muscle and is limited in the posterior region by the ventral region of the incurrent aperture, where the first fringes of the inner margin of the mantle arise.

APERTURES. The apertures of *Fossula fossiculifera* (Fig. 6) are of the A II type (Yonge, 1957). The excurrent aperture corresponds to the anal opening as defined by Ortmann (1921). It is wide with a smooth free border and becomes crenulated depending on the state of contraction. In living animals, the length of the excurrent aperture does not exceed 1 cm beyond the shell margin. The inhalant aperture is separated from the inner lobes of the mantle by a solid connection. The incurrent aperture has a fringed margin, and forms a continuous structure with the pedal opening. The length of the extended incurrent aperture does not exceed 1 cm from the shell margin in living animals buried in the substratum.

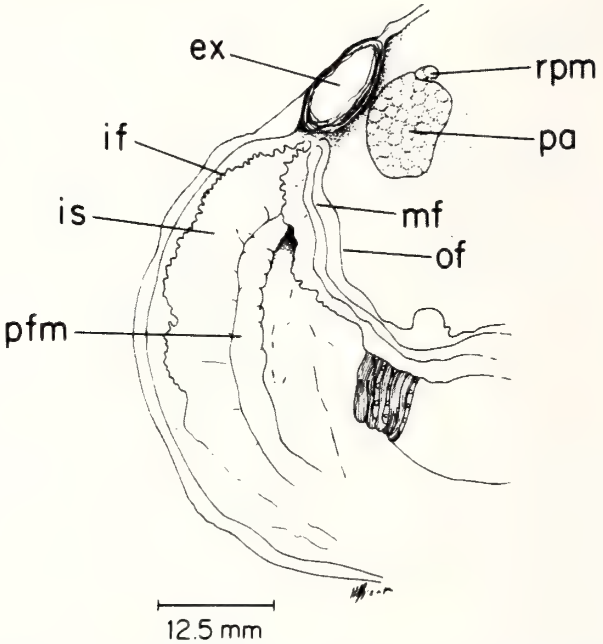

Fig. 6. *Fossula fossiculifera.* Frontal view of incurrent and excurrent apertures showing the posterior fold of mantle (ex, excurrent aperture; if, inner fold; is, incurrent aperture; mf, middle fold; of, outer fold; pa, posterior adductor; pfm, posterior fold of mantle; rpm, retractor posterior muscle).

MUSCLE AND FOOT. The musculature of *Fossula fossiculifera* (Fig. 7) is similar to that of members of Hyriidae

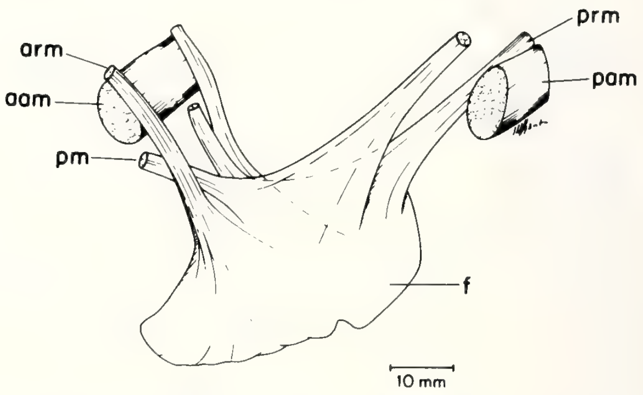

Fig. 7. *Fossula fossiculifera.* Lateral view of musculature after removal of the valves, mantle, palps and visceral mass (aam, anterior adductor muscle; arm, anterior retractor muscle; pam, posterior adductor muscle; pm, protractor muscle; prm, posterior retractor muscle).

and Mycetopodidae described by Mansur (1972), Hebling and Penteado (1974), Hebling (1976), and Avelar and Santos (1991). *Diplodon rotundus gratus, Anodontites trapesialis, A. trapezeus, Castalia undosa undosa* and *F. fossiculifera* all lack ciliation on the foot.

MANTLE CAVITY

Topography. The position of the main organs of the mantle cavity is indicated in figure 8. The visceral mass is yellow and a heavily ciliated region is responsible for rejectory currents that carry particles to the posterior region of the animal. The foot is salmon colored. The ctenidia are yellowish in color and extend posteriorly from the umbonal region to the base of the exhalant aperture. The mantle margins are free, leaving a wide pedal opening. The labial palps (lp) which are large and suboval in shape. The ventral margins of the labial palps are plain and without "sculpture".

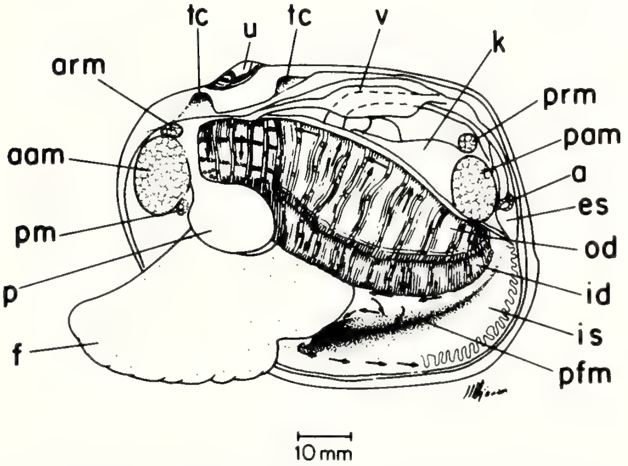

Fig. 8. *Fossula fossiculifera.* Organs and ciliary currents of mantle cavity after removal of left shell valve and mantle lobe (a, anus; aam, anterior adductor muscle; arm, anterior retractor muscle; ex, excurrent aperture; f, foot; id, inner demibranch; is, incurrent aperture; k, kidney; lp, labial palps; od, outer demibranch; pam, posterior adductor muscle; pfm, posterior fold mantle; pm, protractor muscle; prm, posterior retractor muscle; tc, pseudocardinal tooth; u, umbo; v, ventricle).

Labial Palps. The palps of *Fossula fossiculifera* (Figs. 9 and 10) are yellowish in color and symmetrical, with folded inner surfaces and smooth outer surfaces. An area with no folds exists on the inner surfaces of both the anterior and posterior region. The anterior region is connected to the proximal oral groove (pog) and the posterior region to the anterior channel (ac). The food particles that reach the labial palps arrive from the marginal food groove (g) of the inner demibranch, either from the anterior channel that directs particles from the outer demibranchs, or from the anterior mantle groove (ag) that sends the particles from the mantle to the dorsum of the outer labial palps. This last path was observed by Mansur (1972) and Avelar and Santos (1991) in some Hyriidae. The mechanisms of particle screening and acceptance on the part of the labial palps are similar to those observed by Hebling (1976) and Avelar and Santos (1991).

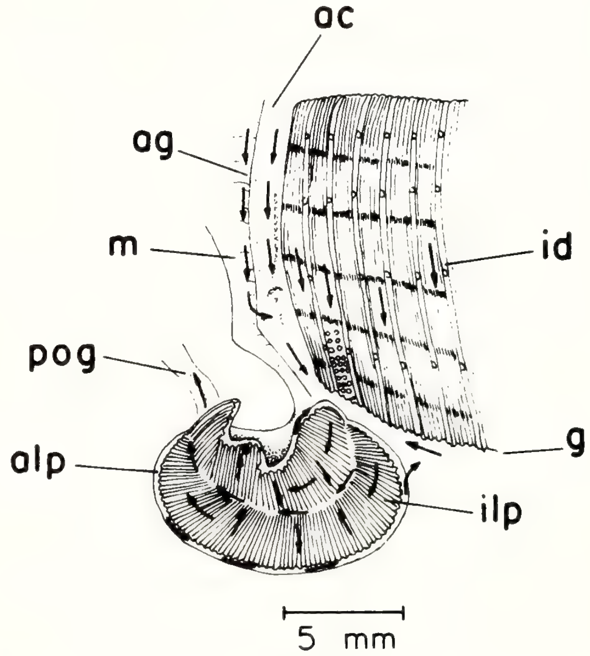

Fig. 9. *Fossula fossiculifera.* Labial palps of left side; arrows show direction of ciliary currents (ac, anterior channel; ag, anterior groove of mantle; g, food groove of inner demibranch; ilp, inner labial palps; m, mantle; olp, outer labial palps; pog, proximal oral groove).

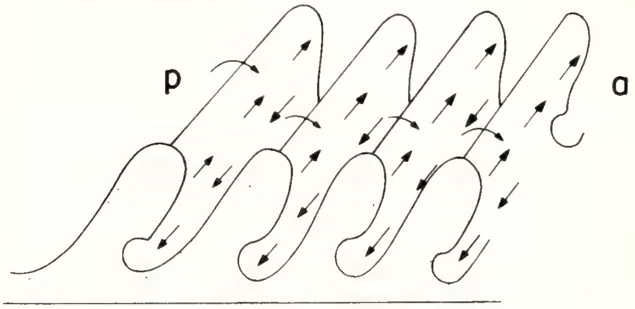

Fig. 10. *Fossula fossiculifera.* Diagrammatic representation of the ciliary mechanisms on the folded inner surface of the labial palps to show the various ciliary tracts (a, anterior; p, posterior).

Ctenidia. The ctenidia of *Fossula fossiculifera* are of type D (Atkins, 1937a), i.e. characterized by the presence of a marginal food groove along the inner demibranchs only. According to Atkins (1937a), this type of ctenidium is characteristic of the Unionidae except *Etheria.*

The ctenidia of *Fossula fossiculifera* are arranged diagonally in relation to the visceral mass. The anterior filaments of the outer demibranchs are smaller than those of the inner demibranch and gradually increase in width posteriorly. The inner demibranch (id, Fig. 8) has approximately six more folds than the outer demibranch, which are clearly visible in the anterior region. The inner demibranch (Fig. 9) grows anteriorly in relation to the mantle and visceral mass, forming a wide and easily visible anterior channel (ac) that ends in the dorsal region of labial palps. The deimbranchs (Fig. 11) are plicate, with filaments varying in number from 17 to 29 in the ascending lamella (alod) and descending lamella (dlod) of the outer demibranch (od). In the inner demibranch (id), the number of filaments in both lamellae (dlid and dlod) is the same as in the outer demibranch.

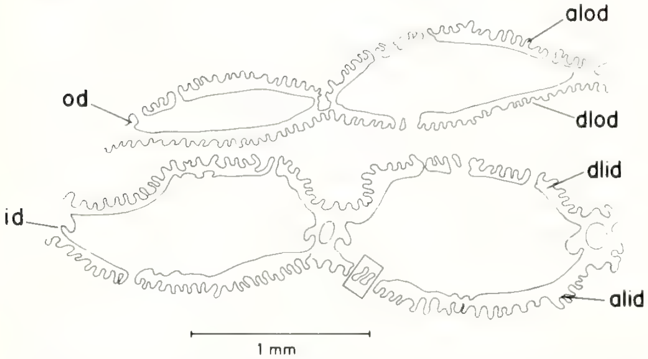

Fig. 11. *Fossula fossiculifera.* Transverse sections through a portion of outer and inner demibranchs showing arrangement of folds and filaments (alid, ascending lamella of inner demibranch; alod, ascending lamella of outer demibranch; dlid, descending lamella of inner demibranch; dlod, descending lamella of outer demibranch; id, inner demibranch; od, outer demibranch; square box outlines two frontal cilia enlarged in figure 12).

In living animals, the characteristic marsupium extends in the inner demibranch and is visible when the animal is brooding the eggs. The ctenidial ciliation of *Fossula fossiculifera* (Figs. 12 and 13) is similar to that of Hyriidae and Mycetopodidae studied by Hebling and Penteado (1974), Hebling (1976) and Avelar and Santos (1991). The frontal cilia (fc) and terminal cilia (tc) are approximately 6.1 µm and 10.4 µm long, respectively, in the inner demibranch. In the outer demibranch the frontal and terminal cilia are approximately 6.1 and 7.7 µm long, respectively. The laterofrontal cilia (lfc) are 18 µm long and the lateral cilia (lc) 14.6 µm long in both demibranchs.

The ciliary currents observed on the branchial surface are illustrated in figures 13 and 14. The screening mechanism of the type described for *Pinna* by Atkins (1937b) was also observed in *Fossula fossiculifera*, with slight modifications (Fig. 15).

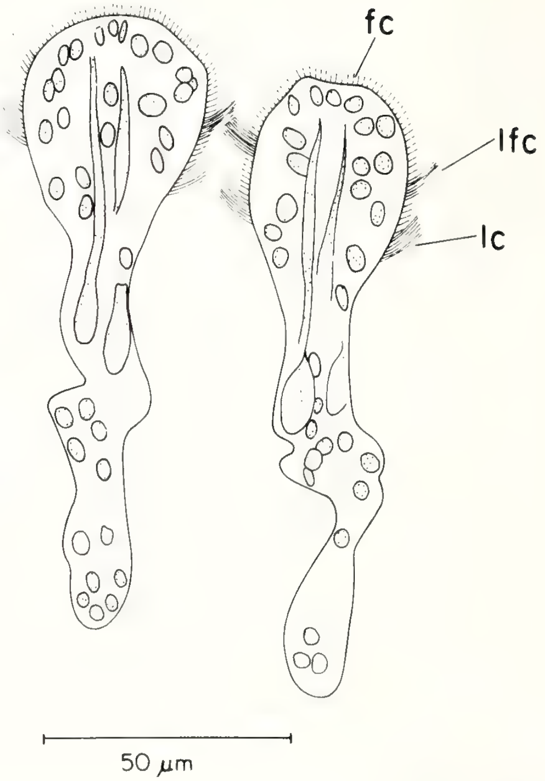

Fig. 12. *Fossula fossiculifera.* Transverse section of two filaments of inner demibranch to show cilia (fc, frontal cilia; lc, lateral cilia; lfc, laterofrontal cilia.

CILIARY CURRENTS OF THE MANTLE. The ciliary currents of the inner mantle surface are divided into two easily visible tracts (tracts 1 and 2) (Fig. 16). The particles that enter the pallial cavity via the incurrent aperture and contact the mantle in the region ventral to the posterior adductor muscle are selected according to weight and size. Small and light particles (tract 1) follow a posterior to anterior direction along a dorsal path between mantle and visceral mass. In the anterodorsal region, the particles follow a ventral direction and reach the outer surface of the outer palp where they are screened and are utilized or rejected. The heavy and/or larger particles (tract 2) are rejected in a dorsoventral direction. These particles reach the posterior muscle fold from where they are directed in a postero-anterior direction. Anterior to this fold, the current contacts the rejection current of the mantle (1), forming an anteroposterior rejection tract where particles move parallel to the free border of the mantle, forming a large rejection tract whose particles are eliminated at the base of the incurrent aperture. This screening mechanism is slightly different from that of Mycetopodidae (Hebling, 1976), Unionidae (Kellogg,

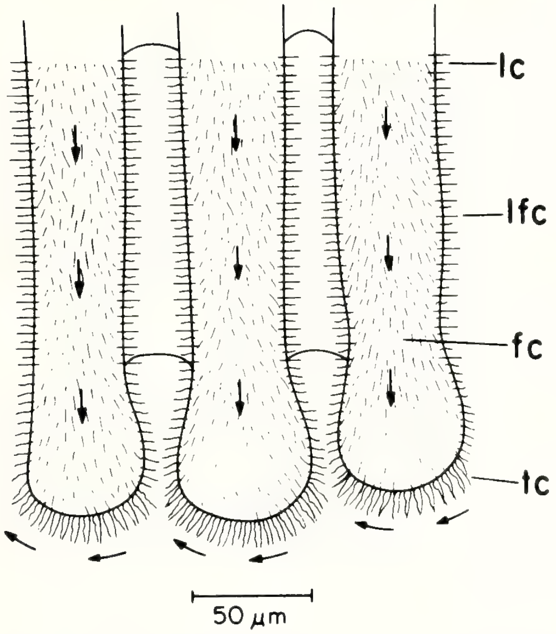

Fig. 13. *Fossula fossiculifera.* Cilia on outer surface of inner demibranch. Arrows indicate direction of ciliary currents, including the oral one (fc, frontal cilia; lc, lateral cilia; lfc, lateral frontal cilia).

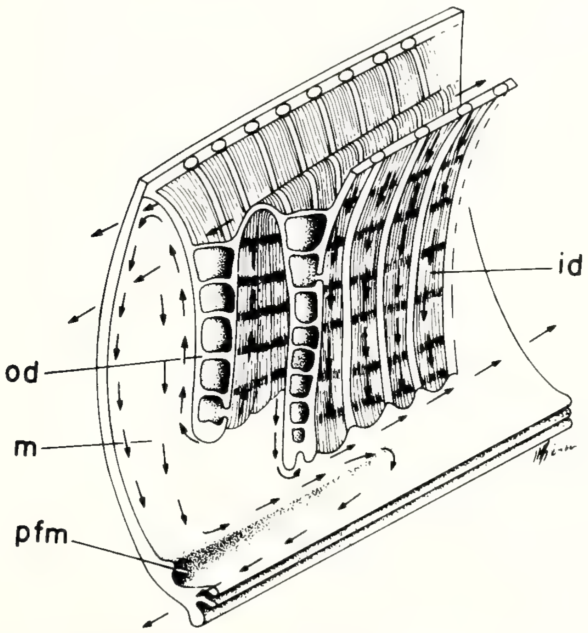

Fig. 14. *Fossula fossiculifera.* Diagrammatic view of mantle and ctenidia. The arrows show the direction of ciliary currents (id, inner demibranch; m, mantle; od, outer demibranch; pfm, posteiror fold of mantle).

1915), and Hyriidae (Hebling and Penteado, 1974; Avelar and Santos, 1991).

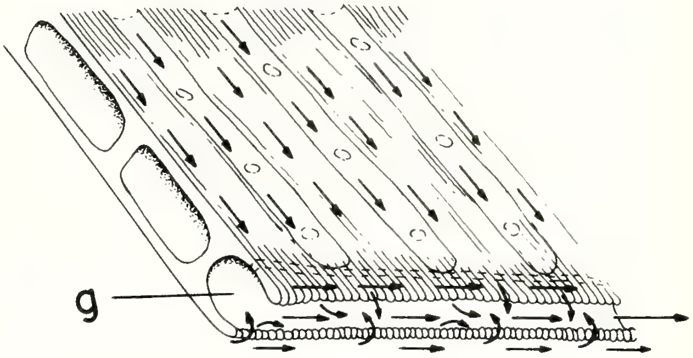

Fig. 15. *Fossula fossiculifera.* Diagrammatic view of edge of the inner demibranch showing the ciliary currents and the marginal groove. The arrows indicate direction of ciliary currents (g, marginal groove).

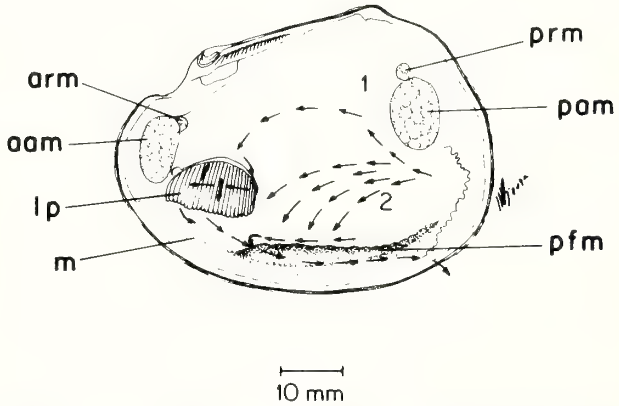

Fig. 16. *Fossula fossiculifera.* Inner surface of right mantle lobe showing ciliary cleansing currents (aam, anterior adductor muscle; arm, anterior retractor muscle; lp, labial palps; m, mantle; pam, posterior adductor muscle; pfm, posterior fold of mantle; prm, posterior retractor muscle; 1 and 2, ciliary tracts).

CILIARY CURRENTS IN THE VISCERAL MASS. The ciliary currents in the dorsal region of the visceral mass run in a ventral direction. At the border between the visceral mass and the foot there is a rejectory tract that sends particles rejected by the labial palps and inner demibranch to the posterior region. The currents running in the ventral direction join those of the rejectory tracts and in this manner the rejected particles are sent toward the posterior end of the visceral mass where they fall in to the rejectory tract of the mantle. Similar rejectory tracts have been detected in the visceral mass of marine bivalves such as the Petricolidae (Narchi, 1975) and freshwater bivalves such as Hyriidae (Avelar and Santos, 1991).

ALIMENTARY CANAL. The general topography of the digestive tract is illustrated in figure 17. The mouth (mo) is located in the posteroventral region of the anterior adductor muscle. The mouth is followed by an esophagus (oe) whose inner wall has grooves and folds that are interrupted at the entrance to the stomach by a transverse ridge (rm) (Fig. 18). The stomach is located in the anterodorsal region of the visceral mass and is enveloped by the digestive diverticula. The stomach of *Fossula fossiculifera* is type IV (Purchon, 1958), as is also the case for Unionidae (Graham, 1949; Purchon, 1958; Dinamani, 1967; Kat, 1983a, b); Mycetopodidae (Hebling, 1976; Veitenheimer and Mansur, 1978; Mansur and Silva, 1990) and Hyriidae (Avelar and Santos, 1991). The general morphology of the stomach, the complexity of the ciliary currents and screening areas and the contiguous intestinal and crystalline style sac (ss) (Fig. 18) apertures are similar to those observed in the bivalve families noted above. However, it should be pointed out that *F. fossiculifera* has a configuration of the right wall of the stomach similar to that of *Bartlettia stefanensis* (Moricand, 1856) and *Anodontites tenebricosus* (Lea, 1834) described by Mansur and Silva (1990). There are three apertures on the right wall of the stomach, a large one in the posterior region, the posterior pouch (pp), that is located in a more ventral position and whose opening into the stomach is marked by the end of the tongue of the minor typhlosole (tm). This duct is adjacent to the screening area (sa3). The second aperture, the anterior pouch (ap), is located in a more dorsal position close to the opening of the esophagus. This aperture is connected to the dorsal hood by a screening area (sa8). The smaller aperture (ddd2) corresponds to the duct described by Purchon (1958) in *Anodonta cygnea*. The stomach configuration observed in *F. fossiculifera* differs from that of *A. cygnea* (Purchon, 1958), *Lamellidens corrianus* (Dinamani, 1967), *A. trapezeus* and *A. trapesialis* (Hebling, 1976) and of the Unionidae described by Kat (1983a, b).

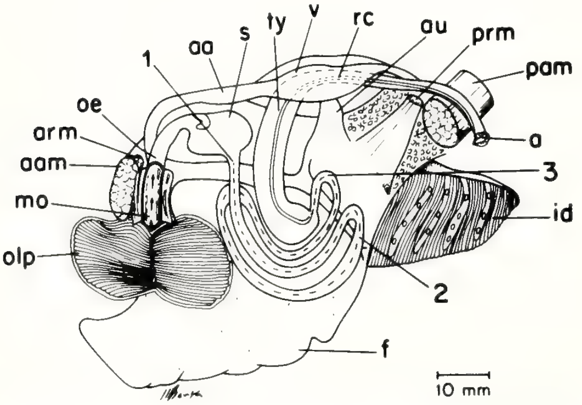

Fig. 17. *Fossula fossiculifera*. Alimentary canal seen from the left side. The numerals 1, 2 and 3 denote major subdivisions in the intestine posterior to the stomach (a, anus; aa, anterior aorta; aam, anterior adductor muscle; au, auricle; arm, anterior retractor muscle; f, foot; id, inner demibranch; mo, mouth; oe, esophagus; olp, outer labial palps; pam, posterior adductor muscle; prm, posterior retractor muscle; rc, rectum; s, stomach; ty, typhlosole; v, ventricle).

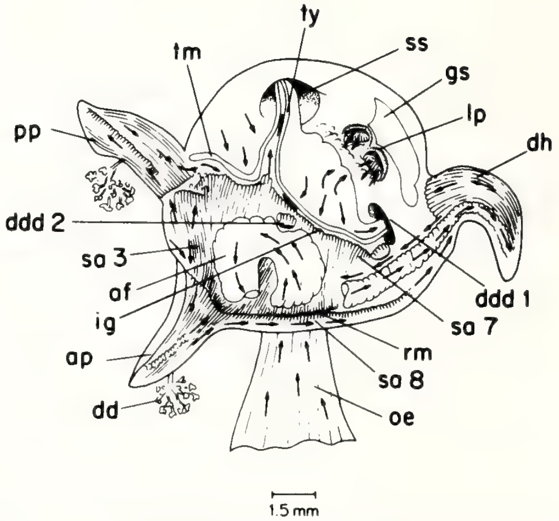

Fig. 18. *Fossula fossiculifera*. Structure of interior of stomach opened by a middorsal incision. Arrows show direction of ciliary current (ap, anterior pouch; dd, digestive diverticula; ddd-1, orifice of left duct of digestive diverticula; ddd-2, orifice of right duct of digestive diverticular; dh, dorsal hood; gs, grastric shield; ig, intestinal groove; lp, left pouch; oe, esophagus; pp, posterior pouch; rm, transverse ridge; sa-3, principal sorting area; sa-7, sorting area below esophageal orifice; sa-8, sorting area on anterior roof of stomach; ss, orifice of style and mid-gut; tm, minor typhlosole; ty, major typhlosole).

Two ducts are easily visible on the left wall (Fig. 18). According to Purchon (1958), these ducts are considered independent, the anterior one being the left pouch. The functioning of the stomach of *Fossula fossiculifera* recalls that of *Anodonta cygnea* (Graham, 1949; Purchon, 1958; Reid, 1965), *Anodontites trapezeus, A. trapesialis* (Hebling, 1976, and *Castalia undosa undosa* (Avelar and Santos, 1991). The intestine of *F. fossiculifera* is divided into three regions exactly as observed in *Acostaea rivoli* by Yonge (1978) and in *Anodontites tenebricosus* and *Bartlettia stefanensis* by Mansur and Silva (1990). The aperture of the style sac is associated with the first region, which extends from the opening of the stomach through a posterior loop of the intestine (Fig. 17, section 1). The second (section 2), consists of two loops of midgut rounded in section with a conspicuous typhlosole. The third (section 3) is an extensive loop terminating in the anus which represents an unusually capacious rectum occupying almost the entire width of the visceral mass and containing an even larger, more oval shaped, typhlosole.

PERICARDIUM, HEART, KIDNEY AND GONADS. The pericardium, heart and kidney (Fig. 8) are similar to those of *Anodonta* (White, 1942). *Fossula fossiculifera* is a hermaphrodite with male and female follicles present at a constant location in the visceral mass. Dissections and serial sections show that as spermatogenic tissue occupies the dorsal and posterior region of the gonad while the oogenic one occupies the ventral and anterior regions of gonad; these distribution is similar a *Anodonta imbecillis* (Kat, 1983c).

DISCUSSION

Studies of the functional anatomy of *Fossula fossiculifera* have revealed the existence of anatomical similarities among the Mycetopodidae, Hyriidae, Etheriidae and Unionidae studied by different investigators. *F. fossiculifera* lives in muddy substrata similar to those inhabited by *Diplodon rotundus gratus* studied by Hebling (1976) and *Castalia undosa undosa* described by Avelar and Santos (1991). In general, studies on freshwater bivalves have shown few special adaptations to a habitat of living close to the surface in relatively soft substrata and feeding on particles in suspension. This fact was also pointed out by Ansell (1961) for marine bivalves. The ability to burrow into soft substratum and occupy the same site for long periods of time, which is a characteristic of both *F. fossiculifera* as reported here, and *Anodontites trapezeus* as demonstrated by Hebling (1976), could be associated with the absence of the dorsal muscle or with the lack of functionality of the dorsal muscle, as observed in *A. trapesialis*, (Hebling, 1976) and *C. undosa undosa*, (Avelar and Santos, 1991).

Fossula fossiculifera has relatively simple papillae in the incurrent aperture. In a study on marine bivalves, Narchi (1972) attributed the simplicity of the siphons to the fact that the animals live in calm waters and feed on particles in suspension. Similarly, *F. fossiculifera* and other freshwater bivalves studied by Hebling (1976), Mansur (1973, 1974), Yonge (1978) and Avelar and Santos (1991) live in calm waters and feed on suspended particles.

The screening mechanism of the *Pinna* type observed in *Fossula fossiculifera* could contribute to more efficient particle selection and utilization. Indeed, when *F. fossiculifera* specimens were placed together with specimens of *Diplodon rotundus gratus, Castalia undosa undosa* and *A. trapesialis* in aquaria under the same conditions, survival time is higher for *F. fossiculifera*, perhaps due to the large amount of food accumulated in the hindgut of the animal. The ctenidia of *F. fossiculifera* are formed by more marked folds than those described by Mansur (1974) for *Monocondylaea minuana* and by Hebling (1976) for *A. trapezeus* and *A. trapesialis.*

A feature that seems to differentiate the Mycetopodidae from the Hyriidae is the arrangement of demibranchial folds. These are more conspicuous in the Mycetopodidae.

The ciliation observed in *Fossula fossiculifera* denotes the living habits of the animals, which prefer muddy environments with fine particles in suspension, such as silt clay and unicellular phytoplankton.

Another adaptation that can be attributed to a muddy type of environment is the marked development of the labial palps which, according to Yonge (1949) is common among animals burrowing in muddy substrata. According to Hebling (1976), the complexity of the ciliary currents in the palps leads to greater efficiency in particle selection. An additional adaptation observed in *Fossula fossiculifera* and perhaps related to more efficient particle selection could be related to the posterior fold of the mantle which overlaps at the point of entry of the incurrent aperture, joining the left side of the mantle to the right side and thus forming a functional canal preventing the flow of incurrent particles from meeting the flow of particles rejected by the mantle, visceral mass, palps and ctenidia. The latter are eliminated in the more ventral region of the incurrent aperture as pseudofeces. It appears that the posterior fold of the mantle also functions as a fourth fold also found in some Tellinoidea, apparently helping remove debris and pseudofeces from the mantle cavity (Yonge, 1948). The posterior mantle fold also occurs in *A. trapesialis*, a fact I have observed in specimens dissected in the laboratory, although Hebling (1976) did not mention its occurrence.

The stomach of *Fossula fossiculifera* and of most freshwater bivalves is type IV (Purchon, 1958), while some freshwater bivalve genera such as *Dreissena* and *Corbicula* have a type V stomach (Purchon, 1960). The stomach of *F. fossiculifera* and its complex ciliary current sorting areas have the same patterns as those of *Anodonta* described by Graham (1949), Purchon (1958) and Reid (1965). However, the stomach of *F. fossiculifera* differs from that of Unionidae and Hyriidae by presenting three apertures on the right wall, two of them large and one small. Hebling (1976) detected only a single digestive diverticulum duct on the right side in *A. trapezeus* and *A. trapesialis.* The stomachs of *F. fossiculifera* and of *Anodontites tenebricosus* and *Bartlettia stefanensis* described by Mansur and Silva (1990) are very similar, especially in terms of the right wall. The greater complexity of the stomach of *F. fossiculifera* could be related to greater efficiency in particle selection.

The general anatomy of the freshwater bivalves show only some differential features, but in the whole, the species are practically identical, furnishes no additional information useful for comprehension of the phylogeny of the genera, except some characters of the shell. Possibly, the posterior fold of the mantle, present in *Fossula fossiculifera* and observed in *Anodontites trapesialis* could reveal a connection between the genera.

Studies performed with species of Mycetopodidae, Hyriidae and Unionidae, show that their similarity results from an adaptive convergence. In spite of being subjected to similar ecological factors, these species exhibit no differential morphological characters, but rather genetic ones (Hebling, 1976).

ACKNOWLEDGMENTS

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Functional morphology of *Heterodonax bimaculatus* (Linné, 1758) (Bivalvia: Psammobiidae)

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Abstract: *Heterodonax bimaculatus* (Linné, 1758) apparently is restricted to the coasts of temperate and tropical America. In southern Brazil, this species occurs infaunally in shallow bay areas on coarse sand substrata. A comparison is made between *H. bimaculatus* and other infaunal Psammobiidae wherein the most significant adaptations concern the organs of the mantle cavity.

The major structural features and ciliary currents are described. Special attention is paid to the ctenidia, labial palps and stomach, and its functional morphology is similar to *Gari* and *Asaphis*. The stomach of *Heterodonax bimaculatus* could not be defined as Type V as exists in all studied Psammobiidae. The major typhlosole does not send a flare into the right caecum but describes a loop very close to the mouth of it. Of all known species of Psammobiidae, only *H. bimaculatus* has a stomach of Type IV. The species can be regarded as being near the ancestral condition in the process of evolution in the Tellinacea and so is at the base of the Psammobiidae lineage.

The genus *Heterodonax* Mörch, 1853, occurs in the West Indies (Keen, 1969), along both coasts of temperate and tropical America (Coan, 1973) and both coasts of Africa (Boss, 1969; Cosel, 1989). *H. pacificus* (Conrad, 1837) was recorded by Coan (1973) and Keen (1971) from southern California to Panama. In the Atlantic, *H. bimaculatus* (Linné, 1758), the type species of the genus, ranges widely throughout the Caribbean (McLean, 1951; Warmke and Abbott, 1962; Keen, 1969, 1971; and Abbott, 1974); Rios (1985) recorded it from Venezuela. So similar is *H. pacificus* to *H. bimaculatus* that most authors consider them conspecific (Keen, 1971).

Heterodonax bimaculatus has been collected rarely along the coast of Brazil; the first record was at São Sebastião Channel, São Paulo, by Ihering (1897). Subsequent records are from Ilha de São Sebastião, São Paulo, by Lange de Morretes (1949) and Rio de Janeiro (Rios, 1985). Although this species commonly is found alive in southern California and northern Mexico, it has not been studied anatomically (Coan, 1973).

Studying the subfamily Tellininae in South African waters, Boss (1969) discussed two species incorrectly placed in the Tellininae: *Scissulina dispar* (Conrad, 1837) and *Heterodonax ludwigii* (Krauss, 1848). Boss (1969) recognized the latter as belonging to the Psammobiidae and gave a diagrammatic illustration of its anatomy.

Isolated references to *Heterodonax bimaculatus* are found mainly in systematics accounts. It is of interest, therefore, to study the functional morphology of this species and to compare it to other psammobiids already known.

MODE OF LIFE

Living specimens were obtained from Praia do Codó, Flamengo Creek, Ubatuba (23°27'S, 45°06'W) on the coast of São Paulo, Brazil. The animals occur in shallow bay areas on the sand substratum (Fig. 1). Like *Gari tellinella* (Lamarck, 1818) and *G. fervensis* (Gmelin, 1791) (Yonge, 1949), they usually inhabit coarse sands, to which they appear to be specially adapted. During high tide *Heterodonax bimaculatus* lives close to the surface in the wave-swept zone, being scoured out of the sand by wave action. The animals are rapid burrowers and have features typically found in organisms that inhabit unstable sediments (Stanley, 1970). The pointed foot emerges from the elongated anterior region of the shell and probes the sand quickly to gain a foothold. Erection of the shell is accomplished by a single burrowing sequence which pulls the animal directly downwards without the rocking movement described for other bivalves, e.g. *Mesodesma mactroides* Deshayes, 1854 (Narchi, 1981).

Heterodonax bimaculatus does not migrate seawards as the tide recedes, but instead they remain high on the beach where they bury deeply looking for moisture. In this condition, *H. bimaculatus* can bury up to ten times the length of its own shell.

Codó Beach has characteristically an upper, shoreward sandy zone and a lower, seaward clay sand zone; the latter becomes exposed only at the lowest tides. On the sand clay zone the water currents inside the bay transfer sand grains from the upper zone and form ripple sand bars.

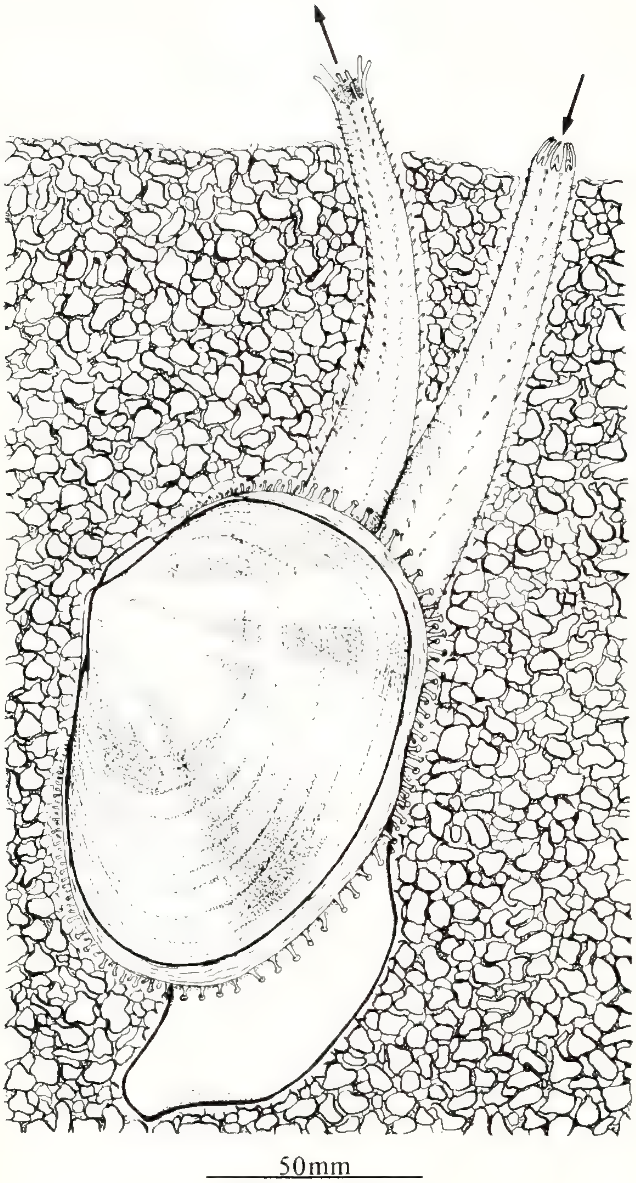

Fig. 1. *Heterodonax bimaculatus.* Animal in natural habitat; exhalent siphon not fully extended. The arrows show the direction of inhalent and exhalent currents.

Heterodonax bimaculatus was first found on this beach by sieving the sand of a ripple sand bar at low tide. Contrary to statements by Abbott (1974) and Rios (1985), *Heterodonax bimaculatus* was not found alive with *Donax* on exposed beaches, as described by Narchi (1978).

MATERIAL AND METHODS

Some behavioral attributes of *Heterodonax bimaculatus* were observed in the natural habitat on the beach at low tide. Live specimens were also kept in aquaria with water and sediment, at room temperature of 21°C, at the Departamento de Zoologia, Universidade de São Paulo, Brazil.

Ciliary currents of feeding and other functional adaptations were observed in live specimens. Studies of the anatomical features and drawings are of living as well as of relaxed and preserved specimens. Magnesium sulphate was used as the relaxing agent. Ciliary currents were studied using carborundum, carmine suspension and graded sand particles. Histological sections (6 to 8 µm thick) were made of tissues fixed in a 10% formalin solution in distilled water and were stained with Ehrlich's haematoxylin and eosin.

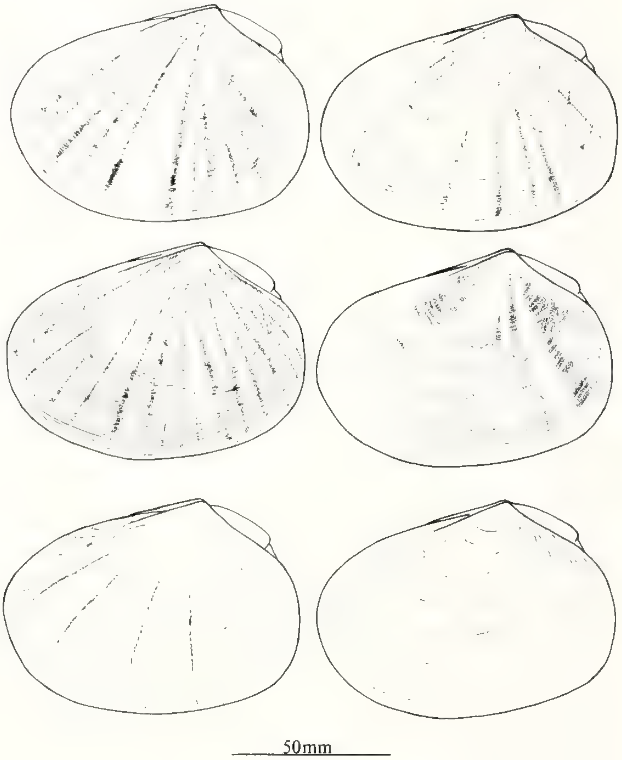

Fig. 2. *Heterodonax bimaculatus.* External view of left shell valves, showing different colour patterns.

SHELL

The shell is bluntly ovate, moderately inflated, inequilateral, thin, fragile, broadly rounded anteriorly and more or less truncate posteriorly. The outer surface of the valves is smoothish and sculptured with fine concentric growth lines (Fig. 2). The hinge plate is thick below the ligament and cardinal teeth and then it is followed by a thinner concave anterior portion. The hinge teeth are relatively large for the size of fully grown specimen. The right valve has two well developed cardinal teeth, the posterior stronger and slightly bifid; the left valve has a large bifid anterior cardinal and a lamellar posterior cardinal (Fig. 3). There are no lateral teeth in either valve. The ligament is external, opisthodetic and rests on a nymph plate. The large "U" shaped pallial sinus, extending from the base of the posterior adductor muscle scar, is broadly rounded anteriorly, irregularly and arcuately extends toward the ventral pallial line which it may or may not meet depending on the specimen. Cruciform muscle scars are not easily discerned.

The valves occur in a variety of colors. They can be white, blue, purple, red, orange, or nearly any combination of these. The color pattern can consist of rays of purple coloration or irregular clouding or flecking. The periostracum is colorless and translucent, but in a few specimens it is yellowish. The shell of the largest animal studied measured 11.4 mm in length, 8.0 mm in height and 5.0 mm in width, and the smallest specimen found measured 4.1 mm in length, 3.0 mm in height and 1.4 mm in width.

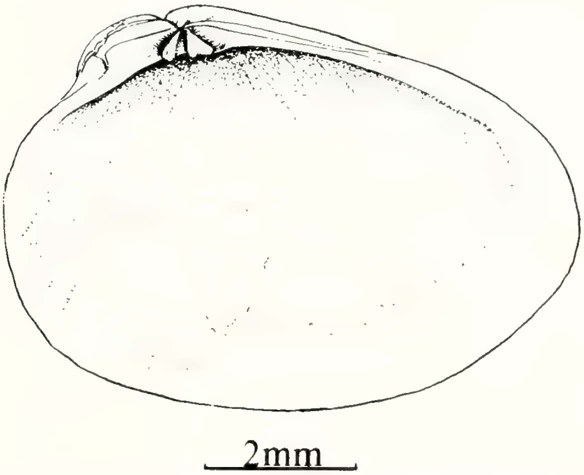

Fig. 3. *Heterodonax bimaculatus.* Internal view of the left valve, showing details of the teeth, ligament, pallial sinus, pallial line and adductor muscle scars. Specimen where the connection of the pallial sinus with the pallial line is absent.

SIPHONS

The siphons are separate and well developed. Their detailed structure is shown in figure 4. The external surface of the exhalent and inhalent siphons bears eight and six longitudinal rows of minute simple and colorless tentacles respectively, underlain by internal, milk-white nerve cords. Both the tentacle rows and the nerve cords are more developed and conspicuous on the ventral and dorsal surfaces than on the lateral surface of the exhalent siphon. The minute tentacles correspond to the sense organs described by Rawitz (1892, cited by Yonge, 1949) for *Gari* and *Solecurtus*. The sense organs are concerned with tactile stimuli or the detection of more delicate water movements.

The orifice of the exhalent siphon is fringed with eight, long, knobbed tentacles, each of which is situated at the distal end of one of the longitudinal rows. The tentacle pairs at dorsal and ventral margin are nearer and more developed than the others. Between the tentacles there are small papillae.

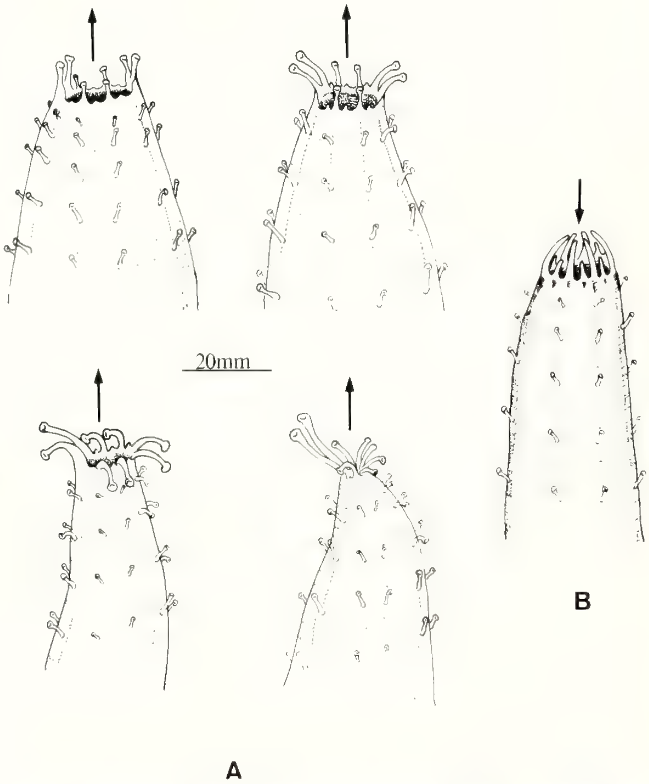

Fig. 4. *Heterodonax bimaculatus.* **A**, appearance of fully extended exhalent siphons, showing movements of the tentacles around their orifices. **B**, detail of the distal end of the inhalent siphon.

The orifice of the inhalent siphon is fringed with twelve tentacles, six of them more developed and situated at the end of the longitudinal rows. The tips of the tentacles are flattened and at its basal region there is a milk-white spot.

Completely buried clams extend their siphons as long as their own shell length. The inhalent siphon extends straight through the substratum keeping its opening a little above the sediment surface. Surrounding suspended material and dense particles lifted from the bottom reach the pallial cavity by the inhalent current. The tentacles can be directed inward to the siphonal aperture creating a feeble barrier against the entrance of large particles; when in clean water they bend outwards.

The exhalent siphon curves dorsally as it extrudes from the substrate; its opening is maintained out of the bottom surface and far from the inhalent. When observed in the laboratory, living specimens protracted both siphons, the exhalent twice or more distance of the inhalent. This condition is maintained even in well relaxed and preserved specimens.

The behaviour of the inhalent siphon during feeding was used, along with other features, by Pohlo (1969) and Reid and Reid (1969) as a criterion for classification of feeding types in bivalves. Later, both Reid (1971) and Pohlo (1982) dedicated more attention to this problem and proposed a more useful criterion for categorizing feeding types.

MANTLE

The two mantle lobes are completely separated, leaving a large pedal gape that extends from the anterior adductor to the cruciform muscle. The middle fold is moderately developed and bears only one row of cylindrical, cup shaped tip tentacles, similar to the ones described by Narchi (1978) for *Donax hanleyanus* Philippi, 1847. The middle folds along with the protraction of the foot and the siphons are extended well beyond the limits of the shell exposing an external surface covered by a thin layer of periostracum.

The inner surface of the mantle is ciliated and its ciliary currents are shown in figure 5. Over a wide dorsal area of the mantle surface the ciliary currents are anteroventrally directed; they carry particles to an anterior convergent area immediately beneath the external labial palp; that area also receives particles from the anterior part of the anterior adductor muscle. Rejection currents are directed ventrally, but a major, powerful rejection tract is situated near the ventral margin, running posteriorly from a point near the anterior adductor muscle to the base of the inhalent siphon.

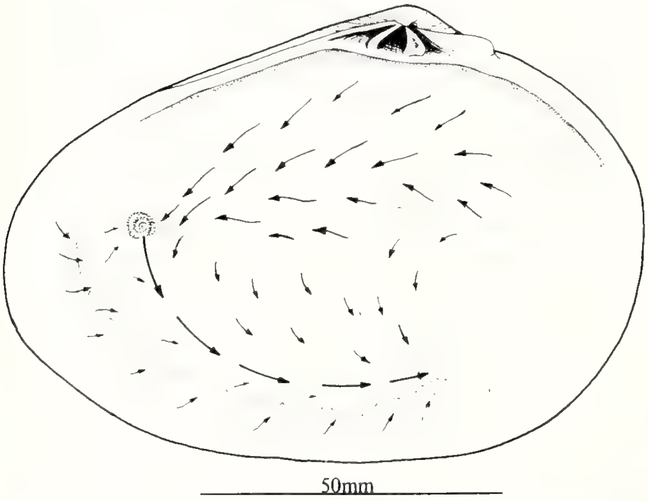

Fig. 5. *Heterodonax bimaculatus.* Inner surface of right mantle lobe, showing ciliary cleansing currents; the arrows show the minor currents and the main rejection tract.

MUSCULATURE AND FOOT

The adductor muscles and pedal musculature are shown in figure 6. The anterior adductor muscle (aam) is elongated and more developed than the posterior adductor (pam), that is transversely oval. The foot is axe-shaped without a flattened sole.There is no aperture of the duct of the byssus gland as Graham (1934a) described for *Gari tellinella*. The foot of *Heterodonax bimaculatus* emerges from the elongated anterior region of the shell to probe the sand and quickly burrow into the substrate, in a similar fashion to that of *Donax hanleyanus* (Narchi, 1978) and of *Mesodesma mactroides* (Narchi, 1981).

The well developed protractor muscles (pm) are attached to the shell juxtaposed to the postero-ventral surface of the anterior adductor muscle. From its insertion on the shell, the protractors pass backwards, twist abruptly as they enter the foot, and spread fanwise to form the outermost muscular layer of the foot.

The two posterior retractor muscles (prm) are inserted on the shell antero-dorsally to the posterior adductor muscle. They pass towards the midline where their bundles of fibers cross each other and split again; the ones coming from the right pass deeply into the left side of the foot, and vice versa, lying internal to the layer formed by the protractor muscle.

The two anterior retractor muscles (arm) are inserted on the shell postero-dorsally to the anterior adductor muscle. Thence they pass ventrally converging so as to form a thick median bundle; without crossing each other, the right and left muscles pass deeply into the foot where they form its innermost muscular layer.

In addition to these muscles, the visceral and ventral parts of the foot present transversely-directed fibres which form a large number of strands crossing from one side to the other. These isolated bundles were considered (Graham, 1934a) to form the true intrinsic pedal muscles.

Despite careful searching no pedal elevator muscles were found in the specimens studied.

The cruciform muscle, characteristic of all Tellinacea (Ihering, 1900), lies at the ventral side of the base of the inhalent siphon. Its morphological features and functions were discussed by Graham (1934), Yonge (1949), Moüeza and Frenkiel (1974, 1976, 1977).

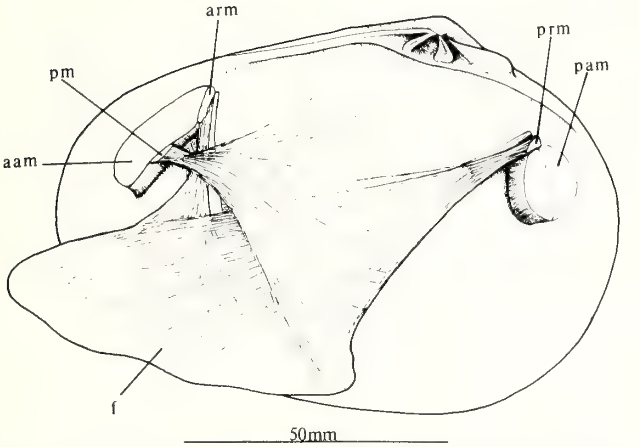

Fig. 6. *Heterodonax bimaculatus.* Diagrammatic representation of the musculature, as seen from the left side (aam, anterior adductor muscle; arm, anterior retractor muscle; f, foot; pm, protractor muscle; pam, posterior adductor muscle; prm, posterior retractor muscle).

CTENIDIA

The arrangement of the organs in the mantle cavity after removal of the left valve and mantle lobe is shown in figure 7. The form of the ctenidia and the general course of the ciliary currents are shown diagrammatically in figure 8. The inner demibranch hangs much lower than the outer and the ascending lamella of the latter rises considerably above the level of the gill-axis, forming a supra-axial extension as Ridewood (1903) described for the Psammobiidae. The inner demibranch is wider than the outer, particularly anteriorly as in *Asaphis dichotoma* (Anton, 1839) [= *A. violacens* (Forsskål, 1775)] (Narchi, 1980).

The ctenidia of *Heterodonax bimaculatus* (Figs. 7, 8, 9) are heterorhabdic with a groove along the free ventral margin of the inner demibranch only. They seem to be like the type C (la) described by Atkins (1937a).

The posterior half of the infra-axial extension and the posterior end of the supra-axial extension of the outer demibranch are shallowly plicate while the rest of the demibranch is smooth. There is no interruption of the cilia at the free edge of the outer demibranch, the appearance is that of a simple bending of the filaments.

On the ascending lamella of the outer demibranch ciliary currents on the smooth area and on the crests and in the troughs between the plicae convey particles toward the free margin. Material is driven around the free margin and toward the gill axis on the descending lamella. Some particles are transferred onto the descending lamella of the inner demibranch.

Unlike the situation in *Asaphis dichotoma* (Narchi, 1980), there is an incipient oralward current along the ungrooved free edge of the outer demibranch. This is due to

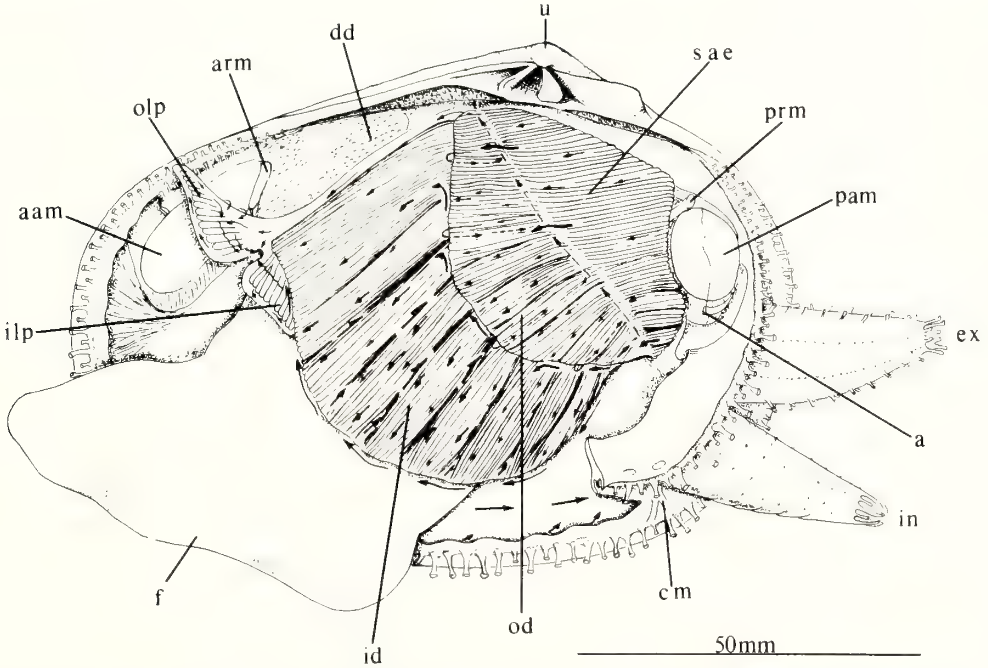

Fig. 7. *Heterodonax bimaculatus.* Animal viewed from the left side after removal of the left shell valve and mantle lobe (the siphons and foot are shown somewhat contracted). Arrows show the direction of ciliary currents (a, anus; aam, anterior adductor muscle; arm, anterior retractor muscle; cm, cruciform muscle; dd, digestive diverticula; ex, exhalent siphon; f, foot; id, inner demibranch; ilp, inner labial palp; in, inhalent siphon; od, outer demibranch; olp, outer labial palp; pam, posterior adductor muscle; prm, posterior retractor muscle; sae, supra-axial extension of outer demibranch; u, umbo).

the presence at the margin of coarse terminal cilia on the posterior half of the frontal surface of each filament; they beat toward the edge and forward, creating a slight longitudinal current or frequently sending particles off the demibranch onto the inner demibranch.

Except for a small smooth anterior portion, the rest of the inner demibranch is plicate. The frontal currents on the descending lamella are directed ventralward on the crest and sides of the plica and dorsalward on the troughs. They are only ventralward on the ascending lamella (Fig. 8). The presence of a dorsalward current makes these gills different from the Type C (1a) of Atkins (1937a) where all the currents are ventralward. Atkins (1937a) included *Gari fervensis* and *G. tellinella* of the Psammobiidae in her Type C (1a) gill ciliation. The number of filaments per plica ranges from 12 to a maximum of 14 at the inner demibranch and 7 to 8 in the outer demibranch.

On each side of the body there are two oralward currents, one in the ctenidial axis and the other in the groove along the free ventral margin of the inner demibranch. Two additional, incipient oralward currents exist; one at the free margin of the outer demibranch and the other at the point where the ascending lamella of the inner demibranch fixes on the visceral mass.

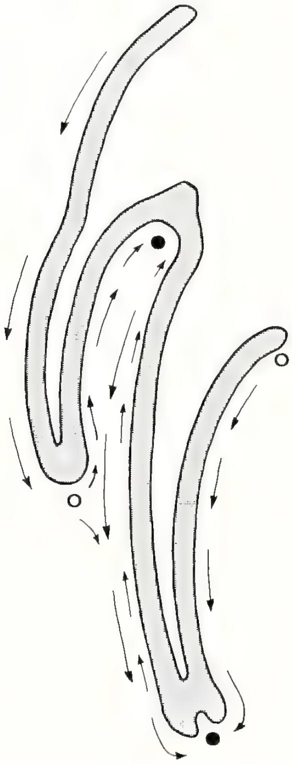

Fig. 8. *Heterodonax bimaculatus.* Diagrammatic transverse section showing the form and ciliary currents on one ctenidium. Arrows indicate the directions of major currents; solid circles, oralward currents and hollow circles, incipient oralward currents.

The 70-116 μm wide filaments (Fig. 9) are separated by 100 μm long laterofrontal cilia (lfc). The lateral cilia (lc) produce a powerful respiratory and feeding current throughout the ctenidia and attain a length of 58 to 68 μm. The 12 μm long frontal cilia (fc) give place to increasingly longer (up to 200 μm) terminal cilia (tc) in the distal ends of the filaments which are placed around the food groove.

A simple row of 170 μm long, stout cilia (rc), is found on the anterior half of the frontal surface of the filaments on both lamellae of the inner demibranch. Each row extends from the free edge of the filament toward the ctenidial axis, attaining a varied length. In some specimens these cilia were present over the lower quarter to a half of the middle part of the inner demibranch, while in the anterior and posterior thirds of the latter they extended but a short distance from the free edge.

Sparse, long (190 μm) frontal cilia (rc_1) were observed at the inner demibranch of *Heterodonax bimaculatus*, similar to those recorded by Narchi (1972a) from the outer demibranch of the venerid *Tivela mactroides* (Born, 1778). The specialized large frontal cilia (rc, rc_1) were not observed on the outer demibranch of living specimens; in preserved specimens it was impossible to recognize them on either demibranch. Along the marginal groove of the inner demibranch a fan-shaped group of long (to 170 μm) guard cilia (gc) are clearly visible. Stout (70-110 μm), cirrus-like cilia (c) are present on the ends of the filaments bordering the marginal groove, mainly at the posterior part of both demibranchs. They beat obliquely forward. Generally there is only one at the tip of each filament.

LABIAL PALPS

The labial palps (Fig. 10A) have the same basic structure and muscular activity as those of *Gari tellinella* (Graham, 1934a) and *Asaphis dichotoma* (Narchi, 1980). The inner face of the labial palps of *Heterodonax bimaculatus* has almost invariably eight folds, whereas there are 12 in *G. tellinella* (Graham, 1934a).

The particles collected on the outer face of the palps are carried to the dorsal margin and then passed to the inner face. The internal, smooth, dorsal margin is relatively wide and its ciliary currents convey particles to the median region of the plicate area of the palp. The inner demibranch of the ctenidium projects deeply between the palps. Particles coming from the inner demibranch and ctenidial axis as well as those collected by the palps from the mantle and visceral epithelium pass to the inner folded surface of the palps.

The sorting mechanisms on the folded surface of the palps (Fig. 10B) carry particles in three major currents,

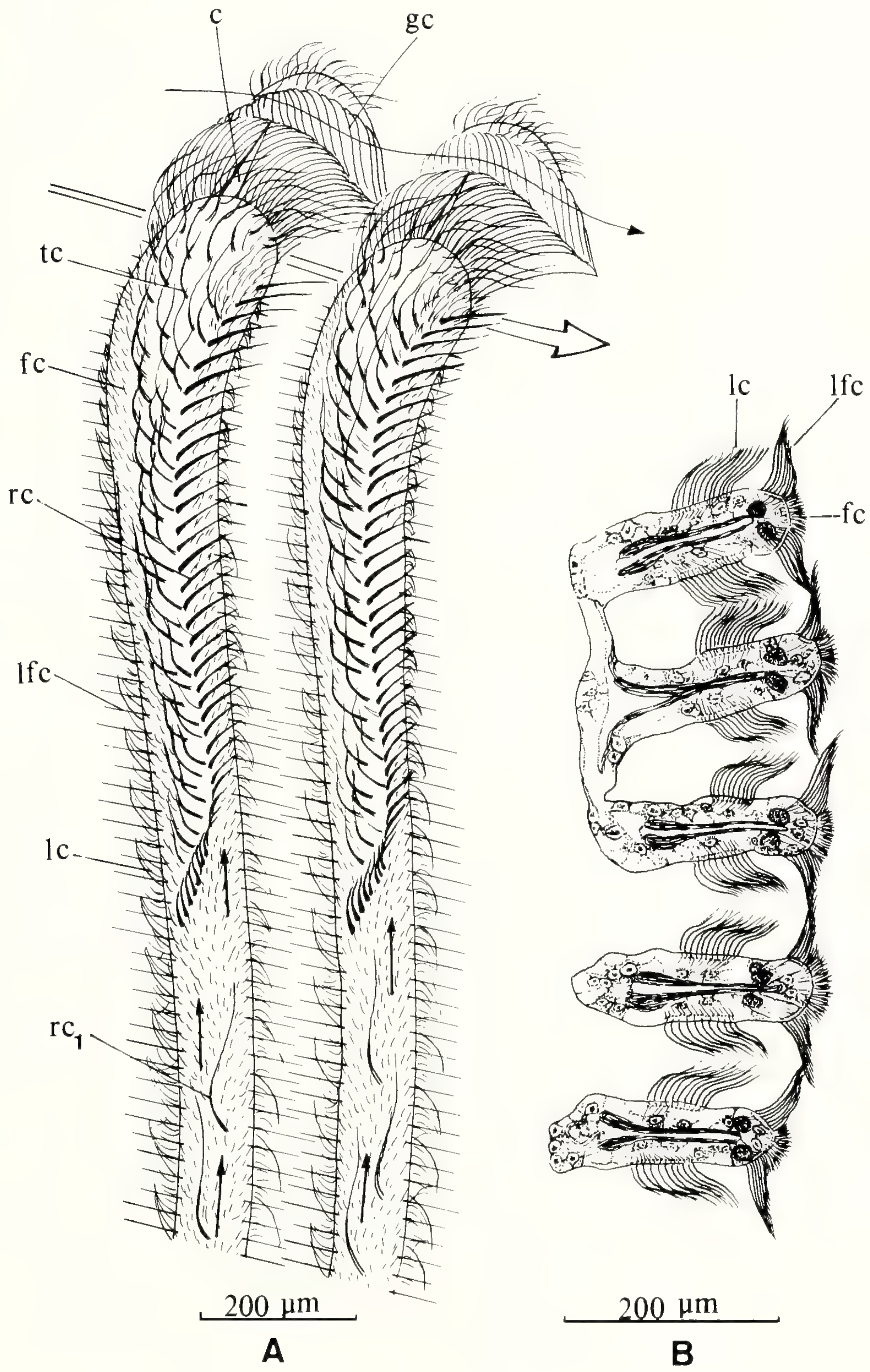

Fig. 9. *Heterodonax bimaculatus.* **A,** distal end of two living filaments of the inner demibranch, showing the arrangement of cilia. Short arrows indicate ventralward currents; long arrows, oralward currents. **B,** transverse section of some filaments, showing the arrangement of the different groups of cilia (c, cirrus-like cilia; fc, frontal cilia; gc, guard cilia; lc, lateral cilia; lfc, latero-frontal cilia; rc, long stout cilia; rc_1, long frontal cilia; tc, terminal cilia).

namely; a powerful current "a", on the aboral side of each plica; particles traveling dorsad on this current are caught by a tract of cilia and throw up to the crest of the plica. Here cilia convey fine particles from crest to crest in an oralward current "c" or throw large ones into the troughs between the folds. In the troughs, rejection currents "b" remove unwanted material onto the smooth ventral margin of the palp, where a vigorous rejection tract carries it to the distal end and on into the mantle cavity. Rejection currents "b" were more intensive on the proximal half of the palps; they were not observed all through the dorsal region of the organ.

These ciliary tracts in *Heterodonax bimaculatus* are similar to those described by Narchi (1980) for *Asaphis dichotoma*, differing only by the absence in the first species of currents at the oral face of the folds.

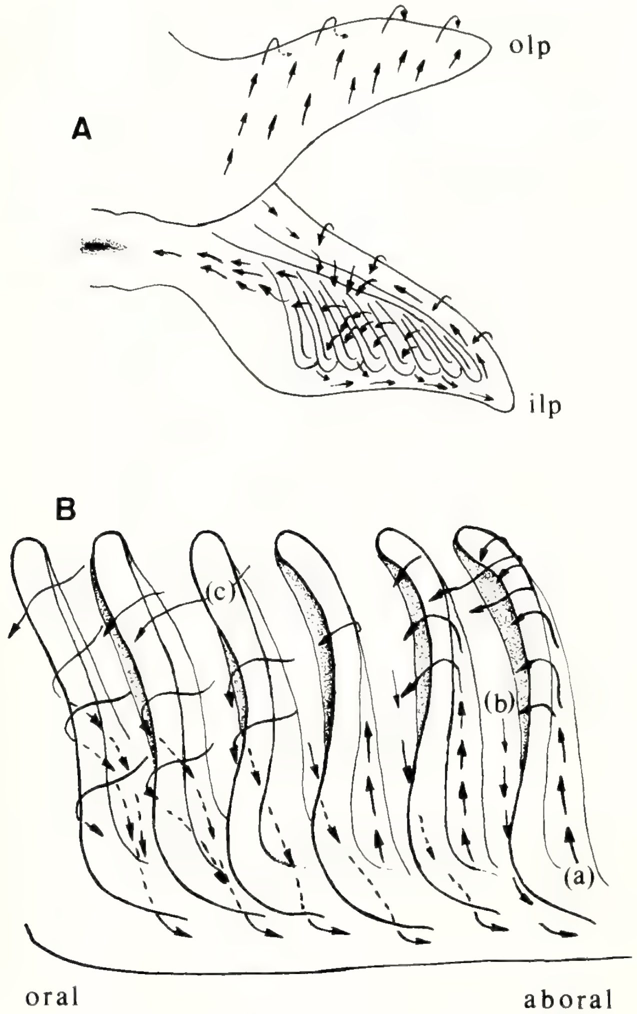

Fig. 10. *Heterodonax bimaculatus. A,* relationship between the inner and the outer labial palps, showing ciliary currents and acceptance tracts (ilp, inner labial palp; olp, outer labial palp). **B,** diagrammatic representation of the ciliary currents on the folds of the inner surface of the labial palp (a, dorsalward current on the aboral side of a plica; b, rejection current at the troughs between the folds; c, oralward current).

The labial palps have an intense muscular activity of their own. They can roll up very easily or contract rhythmically without changing their shape. The inner palps often bend their tip to touch the visceral mass and capture particles on it. The outer labial palps do the same, touching the mantle epithelium.

ALIMENTARY CANAL

The inner demibranch of the ctenidia projects forward between the bases of the inner and outer labial palps. Anteriorly the palps are continuous with the smooth dorsal and ventral lips of the mouth, which have conspicuous muscular movements. Living, dissected specimens were observed to swallow pieces removed from their own ctenidia, muscles or mantle edge. Pieces of tissue as large as the diameter of the mouth were sucked up promptly. Arrival of material between the lips stimulates the mouth to expand and then to close pushing the material backward into the

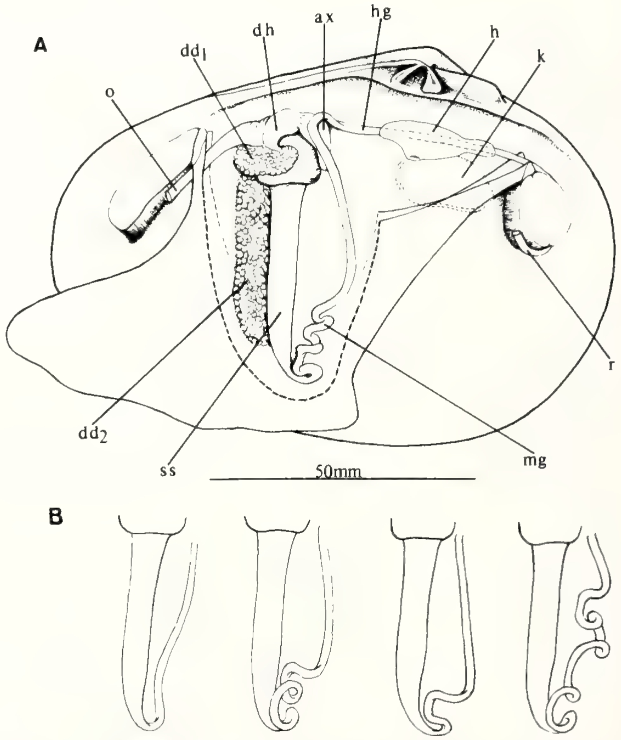

Fig. 11. *Heterodonax bimaculatus. A,* diagrammatic representation of the alimentary canal, as seen from the left side (ax, appendix; dd$_1$, digestive diverticula from the left pouch; dd$_2$, digestive diverticula from the right caecum; dh, dorsal hood; h, heart; hg, hindgut; k, kidney region; mg, midgut; o, oesophagus; r, rectum; ss, style-sac). **B,** four different midgut tracts found in different specimens.

expanding oesophagus. After this, the two anterior retractor muscles contract and pull the foot slightly back. The pressure exerted by the retractors and foot upon the oesophagus forces material into the stomach.

The oesophagus opens into the globular stomach in its anterior dorsal wall. The conjoined style-sac and intestine open into the postero-ventral region of the stomach and pass ventrally toward the foot (Fig. 11A). The midgut arises from the distal end of this wider tube, and ascends parallel to the style-sac and posterior side of the stomach toward the pericardial cavity. In *Gari tellinella*, Graham (1934a) illustrated the midgut separating from the style-sac near its distal end, bending back on itself and, exhibiting two or three closely packed coils, passing along the posterior part of the style-sac towards the hinder-end of the stomach.

Yonge (1949) observed in the Tellinacea that there is considerable variation in the degree of coiling, i.e. in the total length of the midgut. He observed that for *Donax vittatus* and *Gari tellinella* the midgut is quite short. Narchi (1978, 1980) observed the same in *D. hanleyanus* and *Asaphis dichotoma. Heterodonax bimaculatus* has a short midgut which exhibits considerable intraspecific variation (Fig. 11B): straight, or with one to four loose coils before it enters the pericardial cavity via its anterior wall. The hindgut passes through the pericardial cavity, traverses the ventricle and terminates in the anal papilla on the anterior face of the posterior adductor muscle.

STOMACH

The anatomy of the stomach of the genus *Heterodonax* (Fig. 12) is generally similar to that of other members of the Psammobiidae, but it is useful to describe and compare it with *Gari togata* (Deshayes, 1854) and *Asaphis deflorata* (Linné, 1758), adequately studied by Purchon (1960) and with *A. dichotoma* described by Narchi (1980).

The stomach lies dorsally and is surrounded laterally and ventrally by a thick layer of digestive diverticula and gonads. The oesophagus (o) enters the stomach antero-dorsally, its orifice into the stomach being marked ventrally by a transverse, lobed ridge (rm), which represents the swollen extremities of numerous, well defined longitudinal folds. The combined style-sac (ss) and midgut (mg) leave the postero-ventral wall of the stomach. The minor intestinal typhlosole (mt) terminates at the mouth of the midgut. The major typhlosole (ty) consists of two distinct parts. There is a stiff, raised semicircular elevation (e), which curves to the left over the floor of the stomach, the upper surface of which is lined by the gastric shield (gs) and shows no ciliary activity. Under the margin of this shelf, cilia beat strongly towards the orifice of the left caecum (lc); this ridge is not accompanied by an extension of the intestinal groove and cannot be regarded as the major typhlosole as Purchon (1960) defined when describing the stomach of *Gari togata.* The major typhlosole properly arises in the mouth of the midgut and passes forward over the floor of the stomach, accompanied throughout its course by the intestinal groove (ig). Contrary to what was observed with *G. togata, Asaphis deflorata* (Purchon, 1960) and *A. dichotoma* (Narchi, 1980), the major typhlosole does not send a semi-circular tongue into the right caecum (rc). Near to the mouth of the right caecum the major typhlosole forms a semicircular loop, runs transversely across the anterior floor of the stomach, and enters the left caecum (lc). Due to this feature, the stomach of the *Heterodonax bimaculatus* could not be classified as Type V of Purchon (1960). There are five to six ducts of the digestive diverticula opening into the right caecum. At the left caecum there are only three, and one of these ducts receives a flare from the major typhlosole. The major typhlosole extends to the apex of the left caecum, turns back and terminates at the orifice of the left caecum after describing a loose and incomplete spiral of about one and a half turn.

The dorsal hood (dh) is large and well defined, the lower border of its orifice being protected by a very stiff, saddle-shaped sheath of the gastric shield. A broad ridge (r) enters the dorsal hood on the anterior side of its roof, while two parallel slender ridges (r_1, r_2) lie on the posterior side of the roof. Between the ridges r and r_1 there is a ciliated area on which material is driven downward, to the apex of the dorsal hood.

The appendix (ax) is a large and well defined, distensible, conical chamber. It opens into the stomach by a large orifice surrounded by irregularly parallel folds that penetrate deeply into it. The majority of these folds convey particles from the mouth of the dorsal hood inward to the appendix; a few of them, running on the right wall of the stomach remove particles from the appendix onto the style-sac. No sand grains were found inside the appendix. The function of this organ was discussed by Yonge (1949), Purchon (1960) and Reid (1965).

The left pouch (lp) lies antero-ventrally to the opening of the dorsal hood; the posterior border of its mouth is protected by a stiff, saddle-shaped flare of the gastric shield. The left pouch passes backward under the dorsal hood. About nine ducts enter the left pouch from the digestive diverticula on the left side of the body. A sorting area of extremely fine striations (sa_6), divided into two bands, lies on the left anterior floor of the stomach and penetrates deeply into the left pouch. One band runs close to the wing of the gastric shield; at the distal end of the left pouch its striation invades the aperture of ducts of the digestive diverticula. The other band runs at the anterior wall of the left pouch where remaining ducts open. The ciliary currents on

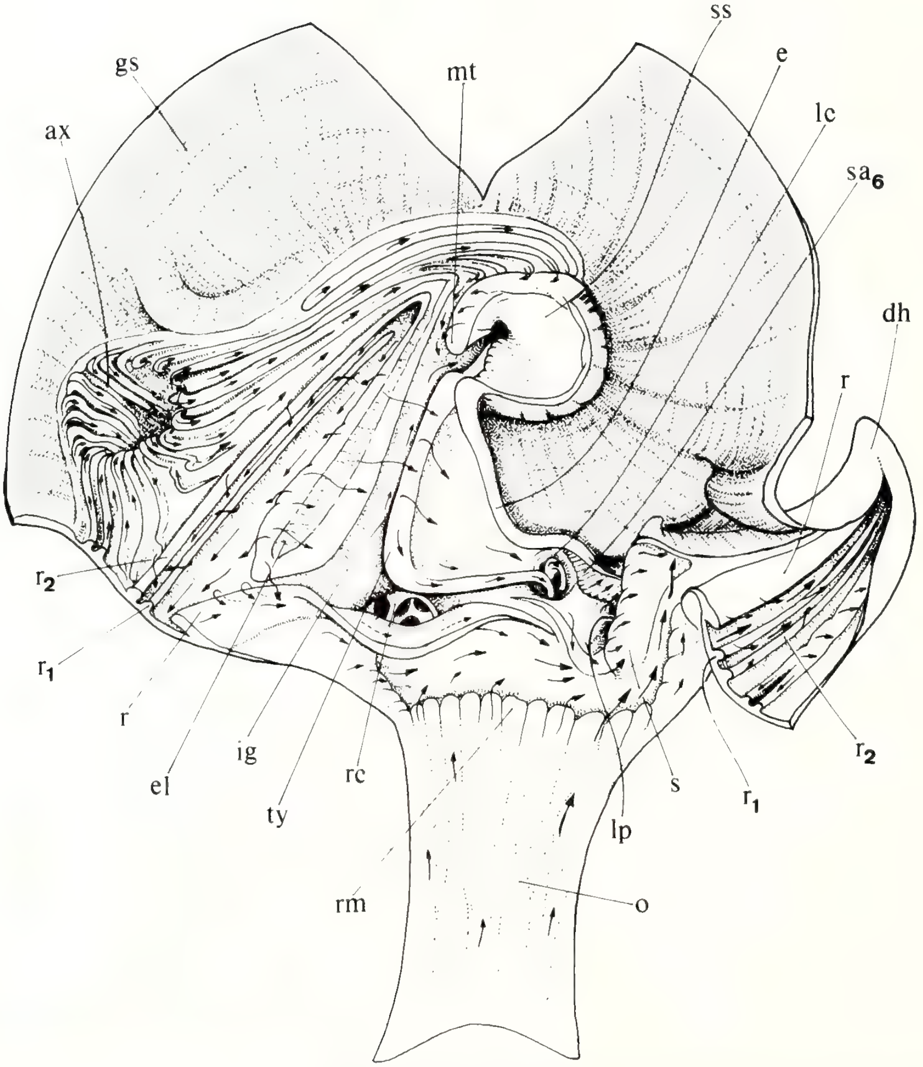

Fig. 12. *Heterodonax bimaculatus.* Interior of the stomach after its opening by an incision in the dorsal wall (ax, appendix; dh, dorsal hood; e, raised semicircular elevation; el, long forwardly projecting tongue; gs, gastric shield; ig, intestinal groove; lc, left caecum; lp, left pouch; mg, midgut; mt, minor typhlosole; o, oesophagus; r, broad ridge; r_1, r_2, ridges on the posterior wall of the dorsal hood; rc, right caecum; rm, rim to the oesophageal orifice; s, swelling of the left anterior wall of the stomach; ss, style-sac).

these two regions of sac always convey particles dorsalward; at the apertures of the ducts, cilia beat outward.

A broad swelling (s) on the left anterior wall of the stomach isolates the apertures of the left pouch and dorsal hood; its ciliary currents remove particles from the mouth of the left pouch into the dorsal hood. Together with the broad ridge "r" it forms an efficient barrier against the free passage of material coming from the oesophagus to the cavity of the stomach. Reaching the ridge "r", isolated particles from the oesophagus are driven to the left, then into the dorsal hood via a ciliary tract on the dorsal side of the broad swelling (s).

The parallel ridges "r_1" and "r_2" emerging from the dorsal hood pass downward over the roof and right wall of the stomach ending up near the opening of the midgut. A "U"-shaped ventral tongue (el), similar to those described in *Gari togata, Asaphis deflorata* (Purchon, 1960) and *A. dichotoma* (Narchi, 1980), lies to the right and ventrally to ridges "r_1" and "r_2". The particles on its dorsal margin are driven to the gutter between "el" and "r_1" and then to the dorsal hood. Elsewhere, the cilia on the tongue pass particles to the intestinal groove (ig) or over the major typhlosole and then either to the right or left caecum.

The crystalline style projects into the stomach and is brown in colour. In living dissected animals with stomach, appendix and dorsal hood empty, the crystalline style could be seen through the stomach wall.

A few seconds after adding carmine suspension to the pallial organs, a red mucous strand reached the stomach. Rotation of the style causes the material to be carried downward, toward the floor of the stomach. The crystalline style rotates in a clockwise direction when viewed from the anterior end, and the observed speed varied from 13 to 16 r.p.m. at 20°C and attained 26 r.p.m. at 21.5°C. Five minutes later, the red particles were driven by cilia from the floor and right wall of the stomach to the dorsal hood. Next, the appendix started to become red, giving clear evidence that it received particles from the dorsal hood. Thirty minutes after the beginning of the experiment, the foregut was stained red.

An extremely viscous mass with amorphous material was observed within the stomach of living dissected specimens and in fixed animals. The viscous mass that filled the stomach extended to all corners of this organ and few mineral grains (up to 0.2 mm) and entire diatoms (0.08 mm) were found.

DISCUSSION AND CONCLUSIONS

Heterodonax bimaculatus is an intertidal species living shallowly buried in sand or gravelly sand, in protected bays. A similar habitat is occupied by *H. ludwigii* (Boss, 1969) and *H. pacificus* (Keen, 1971; Coan, 1973). Broekhuysen and Taylor (1959 cited by Boss, 1969) obtained *H. ludwigii* in a sand bar in the estuary at Kosi Bay. According to Boss (1969), this latter species has "a preference for estuarine conditions with a considerable amount of suspended matter". At Codó Beach, the circulating water inside Flamengo Creek often keeps a large amount of fine organic matter in suspension.

As in the species of *Gari*, representative of the British seas (Yonge, 1949), *Heterodonax bimaculatus* seems to be specially adapted to the sandy or sandy gravel substrata, because it occurs only intertidally on Codó Beach. Its presence on the ripple sand bars formed on the sublittoral zone could be accidental. Specimens buried on the border between the sand beach and clay sand zone, or those less efficient in their ability to burrow quickly in the sand zone, could be scoured out of their natural habitat and transported into the sublittoral.

Heterodonax bimaculatus presents some features typically found in clams that inhabit unstable sediments. As with *Donax hanleyanus* (Narchi, 1978) and *Mesodesma mactroides* (Narchi, 1981), it has a wedge-shaped smooth shell and a well developed and active foot. The elevator pedis muscle, characteristic of these high speed burrowing bivalves and correlated with the habit of burrowing in firm sand (Yonge, 1949; Narchi, 1978), is lacking in *H. bimaculatus*.

Atkins (1937a) classified *Gari tellinella* as a deposit feeder; Yonge (1949) observed the inhalent siphon of this species and *G. fervensis* opening widely for the passive intake of loose surface deposit and suspended material. Conflicting statements concerning the nature of feeding in the Tellinacea received exhaustive consideration by Pohlo (1969, 1982), Reid and Reid (1969) and Reid (1971).

According to the criteria for feeding types in bivalves, *Heterodonax bimaculatus* is a suspension feeder, more precisely a non-selective suspension feeder in Pohlo's (1982) classification. The clam possesses large ctenidia relative to the labial palps, which are small and characteristically with few folds; the outer demibranchs are not reflected although they are provided with a wide supra-axial extension; ctenidia type C (la) (Atkins, 1937a) (slightly modified) with a well-developed marginal groove on the inner demibranch; a waste canal (Kellogg, 1915) absent; a vertical orientation in the burrow and only finger-like non straining tentacles around the inhalent aperture.

As in the donacids *Egeria radiata* (Purchon, 1963), *Iphigenia brasiliensis* (Narchi, 1972) and *Donax* itself (Yonge, 1949), the siphons of *Heterodonax bimaculatus* are relatively shorter and wider compared with most extant tellinaceans (particularly the deposit feeders Tellinidae, Scrobiculariidae and some Semelidae). In the species with shorter and wider siphons the inhalent current caused by the beating of the lateral cilia on the ctenidia is less concentrated and correspondly less powerful (Yonge, 1949). *H. bimaculatus* is unable to tear off bottom material and suck it in actively as do the specialized deposit feeders, hence the clam deals with less pseudofaeces and these are expelled by the usual route, through the inhalent siphon, without the protection of a pair of folds that prevent the pseudofaeces from being washed forward by the very concentrated inhalent current.

In addition to the loss of ramified straining tentacles, the passive behaviour of the inhalent siphon which is kept well clear from the sediment surface seems to corroborate the suspension feeding habit of *Heterodonax bimaculatus*. Despite this, the clam may derive part of its nutritional requirements from loose surface deposits as well as from the dense deposited material. This latter is achieved passively when the inhalent aperture is kept widely open, or at slightly below, the sediment surface. At these times surrounding benthic organisms and sand grains may fall into the pallial cavity.

The presence of specialized large frontal cilia (rc,

rc_1) on the frontal surface of the filaments of the inner demibranchs is evidence that *Heterodonax bimaculatus* deals with large particles inside its pallial cavity. These stout frontal cilia are undoubtedly a specialization for removing unwanted material, such as sand grains from the lamellae (Atkins, 1937; Narchi, 1972). The bivalves described as possessing them are all sand dwellers, silty sand dwellers or borers in rock or wood (Atkins, 1937). These cilia in *H. bimaculatus* seem to be efficient in their function since only few and minute (up to 0.2 mm) mineral grains were found inside the stomach of one specimen examined for this purpose.

In *Heterodonax bimaculatus* the marginal groove on the inner demibranchs possesses fine guard cilia in common with *Gari tellinella* and *G. fervensis* (Yonge, 1949) and a wide variety of other Filibranchia and Eulamellibranchia listed by Atkins (1937), most of which inhabiting silty or muddy substrata. According to this author, guard cilia are presumably efficient in dealing with the particles of a muddy soil, but not sufficiently robust when coarse material has to be dealt with.

At Codó Beach not only the layer subjacent to the superficial clean sand contains a large amount of silt but so does the circulating water, which may sporadically remove and transport mud particles from the sublittoral zone. Having both large frontal and guard cilia, *Heterodonax bimaculatus* is adapted to deal simultaneously with fine and coarse material present in its environment.

The observations made in the laboratory with the clam ingesting pieces of their own tissues, suggests that it is able to regulate the sorting mechanisms in the pallial cavity. Submitted to a dense inhalent current the animal can reject the excess of material. If the surrounding water is scanty in food material *Heterodonax bimaculatus* can retain and ingest even those large particles usually rejected. The small size of the palps and their reduced number of sorting folds could represent a simplification to facilitate an acceptance of large particles.

The large ctenidia of *Heterodonax bimaculatus* are responsible for the principal selection before material is passed to the palps; so, the palps could be maintained as small as possible with little contribution to the sorting devices inside the pallial cavity. The intense muscular activity of the palps, which roll up or bend at the sides to touch the visceral or mantle epithelium, contributes respectively to discharge the excess of material or to capture useful particles travelling ventralward on those epithelia.

Some species of the Psammobiidae were classified as deposit feeders by Hunt (1925) and Atkins (1937a), non-selective by Pohlo (1982) or even suspension feeders by Yonge (1949). According to Pohlo, the non-selective feeding type as observed in the family Solecurtidae and Psammobiidae and in some species of the Donacidae, represents an intermediate stage of the evolution of the tellinaceans from a selective suspension feeding ancestral to a final stage represented by the specialized deposit feeders.

The alimentary canal of *Heterodonax bimaculatus* is similar to that of *Gari tellinella* (Graham, 1934a), and the stomach resembles that of the Tellinidae and Semelidae (Yonge, 1949) in relation to the presence of a straight style-sac with an associated intestinal groove and in the presence of an appendix. The internal anatomy of the stomach resembles that of *G. togata* and *Asaphis deflorata* studied by Purchon (1960) and *A. dichotoma* described by Narchi (1980), differing only in a few aspects.

The large and distensible appendix of *Heterodonax bimaculatus* differs from that of *Gari togata*, described by Purchon (1960) as a pear-shaped chamber opening into the stomach by a slender, smooth walled neck. Purchon (1960) and Narchi (1980) referred to the appendix of *Asaphis deflorata* and *A. dichotoma*, respectively, as a capacious sac, with the opening into the stomach guarded by two large flashy pads and flanked by two sorting areas (SA 11) of irregularly parallel folds, which do not penetrate into the appendix. Ciliary currents in that sorting area beat inward, passing material into the appendix; no outward ciliary currents were found by these authors. *H. bimaculatus* presents all around the mouth of the appendix only parallel folds penetrating deeply into the organ. Outward ciliary activity was detected on some of those parallel folds running on the right wall of the stomach.

As stated by Purchon (1960) and confirmed by Reid (1965), the real function of the appendix is for temporary storage of exceptionally large particles which have escaped rejection by the sorting mechanisms of the pallial cavity. In *Heterodonax bimaculatus*, very fine particles of carmine were found in the appendix. Its emptying is carried out by ciliary activity and it is possibly aided by muscular contraction of its walls, as proposed by Purchon (1960) for *Asaphis deflorata.*

In the stomach of *Heterodonax bimaculatus* there are not bead-like swellings in front of the broad ridge "r" which extends up to the right wall of the stomach into the dorsal hood, as well as any series of shallow blind pockets close to the mouth of the style-sac and midgut, present in *Gari* (Purchon, 1960).

Purchon (1960) stated that the type IV stomach is more primitive and possibly ancestral to type III and type V stomachs. Through a process of "juvenilization", i.e. by a reduction in size of individuals accompanied by a general simplification of parts of the organs, which if including a withdrawal of the tongues of the major typhlosole from association with the ducts of the digestive diverticula, stomach type V could revert to the ancestral type IV. According to Purchon (1960), this theory could be advanced to account for the occurrence of a type IV stomach in the eulamellibranch families Sphaeriidae, Thyasiridae and in *Chama multisquamosa* (Chamidae). The type IV stomach of *Heterodonax bimaculatus* could represent a similar, and so far the only known, such reversion in the Psammobiidae.

In a revision of the basic form and adaptations of the Lucinacea, Allen (1958) admitted the occurrence of a simplification in the stomach of Thyasiridae and Lucinidae, accomplished by the loss of sorting areas and reduction of the number of apertures leading from the stomach to the digestive diverticula and an increase in the size of these apertures. This simplification occurred to facilitate the acceptance of large particles, since the animals live in an environment where the food supply is so low that all available particulated food has to be accepted. Thus the findings of Allen (1958) for the Lucinacea fit in well with the views expressed by Purchon (1960).

The simplicity of the stomach of *Heterodonax bimaculatus* expressed by the presence of only a few and poor sorting areas, in addition to the simplicity of the labial palps and the voracity exhibited in the laboratory, suggest a convergence with the Lucinacea. Purchon (1960) considered the paucity and the simplicity of the sorting areas of the stomach of *Gari togata* as being probably correlated with the unusually high viscosity of the stomach contents, which prevents individual particles from being brushed against the ciliary sorting area.

According to Pohlo (1982), the type IV stomach is also the ancestral condition from which the type V stomach evolved. This point of view is supported by the presence in the extant Donacidae *(Donax)*, which he considered as retainers of more ancestral features of a type IV stomach. From a *Donax*-like stage with a selective mode of suspension feeding, evolution then proceeded to less selective suspension feeding as seen in some Donacidae and also in the Solecurtidae and Psammobiidae. The stomach also shows an advance to type V (Pohlo, 1982), a stage present in some of the Donacidae, e.g. *Donax trunculus* (Moüeza and Frenkiel, 1976), *Egeria radiata* (Purchon, 1963), *Iphigenia brasiliensis* (Narchi, 1972) and *D. hanleyanus* (Narchi, 1978). This stomach type then remains throughout the rest of the superfamily (Pohlo, 1982).

From Pohlo's (1982) point of view, *Heterodonax bimaculatus* can be regarded as being near the ancesteral condition in the Tellinacea and so, at the base of the Psammobiidae lineage, since it has retained a type IV stomach and the majority of its anatomical features relate to a selective suspension feeding behaviour except in the absence of straining tentacles around the inhalent aperture.

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Origin and decline of the estuarine clam *Rangia cuneata* in the Neches River, Texas

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Abstract: The origin and decline of the brackish water clam, *Rangia cuneata* (Gray, 1831), in the Neches River were investigated by records of navigation improvements, salt water encroachment, water quality, and demographic data. The origin was probably very recent (since 1900) resulting from construction and improvements to the deep water navigation channel. These modifications formed a suitable salinity environment and allowed the planktonic larvae to be carried upriver from Sabine Lake. By 1951, after industrialization along the navigation channel, all *Rangia* beds located below river km 40.5 had been eliminated by wastewater effluents and frequent dredging. In 1971, the *Rangia* population consisted of 45 beds located between river km 40.5 and 57.3. The average density was 238 clams/m^2 and the total area of the beds was 113, 115 m^2. Since 1971, many *Rangia* beds have disappeared and all remaining beds examined exhibited decreased density to <1 to 2 clams/m^2 with an increase in average clam size. These changes were due to alterations in the river discharge pattern that decreased the frequency of salt water intrusion required for spawning and survival of larvae, and natural and cold weather mortalities. By 1985, the permitted BOD waste load in the lower river had been reduced 96%, but *Rangia* has not yet recolonized this section of the river.

Rangia cuneata (Gray, 1831) is an important estuarine bivalve (family Mactridae) that is distributed from Maryland to Florida along the Atlantic coast and from northwestern Florida to Campeche, Mexico along the Gulf of Mexico (Hopkins and Andrews, 1970; Andrews, 1971). *Rangia* is a permanent resident in the oligohaline (0.5-5 ppt) and mesohaline (5-18 ppt) regions of estuaries and is often the dominant species in terms of biomass (Odum and Copeland, 1969; Cain, 1975). *Rangia* converts organic detritus and algae into organic biomass which can be utilized by many secondary consumers, including crustaceans, fishes, water fowl, and humans (LaSalle and de la Cruz, 1985). The shells are used for construction and manufacture of many industrial products (Hopkins and Andrews, 1970; Gooch, 1971) and provide a suitable substratum for attachment of epifauna (Hoese, 1973). In addition, *Rangia* is an excellent biomonitor of some hazardous substances, including the metals cadmium, chromium, copper, and lead, as well as the chlorinated hydrocarbons dioxins and furans (Harrel and McConnell, unpub. data).

Cain (1973, 1975) and Hopkins *et al.* (1973) reported that the distribution of *Rangia* populations is due to factors that control spawning and survival of the larvae, not adult physiology. They reported that gametogenesis was stimulated by temperatures around 15°C or higher, but spawning would not occur unless salinity changed, up from low salinity or down from high salinity. If salinity change does not occur, the gametes will undergo cytolysis when the temperature decreases to about 17°C. Once spawning occurs, early larvae will not survive unless the salinity is between 2 and 10 ppt. However, after the larvae have developed past the planktonic stage and settled to the bottom, salinity is no longer a critical factor. Fairbanks (1963) reported an average life span of eight years and Hopkins *et al.* (1973) established a maximum life span of 15 years; thus, larval recruitment to populations can occur at long time intervals. Established beds of *Rangia* are concentrated where salinity seldom exceeds 18 ppt (LaSalle and de la Cruz, 1985) and have never been reported where salinity is continually higher than 15 ppt (Hopkins *et al.*, 1973).

Many investigators have reported on the distribution and abundance of *Rangia* in different estuaries and on various aspects of its physiology. These studies were reviewed by Hopkins *et al.* (1973) and LaSalle and de la Cruz (1985). However, no long term studies on a single population of *Rangia* have been conducted, but are necessary to understand how anthropogenic changes and natural environmental variations affect the distribution and abundance of the species. This study traces the environmental history, origin, and decline of *R. cuneata* in the Neches River estuary of Texas. The results substantiate information from other studies and yield new information on the ecology of this important species.

METHODS

The historical distribution of *Rangia cuneata* was postulated by correlating ecological requirements of the species with the environmental history of the Sabine-Neches estuary. Modern distribution of *Rangia* was established by locating and sampling beds along the entire length of the Neches River estuary in 1971. Individual beds were located by sighting dead shells along the shoreline and by probing the bottom with a metal rake from a small boat. When a bed was located, clams were retrieved by hand to determine if they were alive. Only live beds were studied, but the presence of dead beds was noted. The length and width of all live beds were measured and all clams from several quadrats (30.48 cm x 30.48 cm) were removed by hand for determination of density and size distribution. The number of quadrats sampled per bed varied (6 to >30) with the size of the bed and the density of the clams. The quadrats were located at various intervals along the entire length of the beds in water 30 cm to 1.5 m deep. Characteristics that delineated bed boundaries (i.e. depth, change of substratum, or physical barriers) were noted. The greatest length of all clams, or of the first 500 to 600 clams collected from the quadrats, was measured to the nearest mm with vernier calipers or with a measuring board.

Density and size distribution of clams at Bed 2, located at river km 40.5, were determined in 1969, 1971, 1977, 1978, 1981, and annually thereafter. One meter square quadrats were used during these analyses and the number of quadrats sampled varied from three during 1969, the year of highest density, to 18 in 1991, the year of lowest density. The number of quadrats sampled during other years varied from five to 15. Additional data on density and size distribution were collected at Bed 10, located at river km 48, and Bed 45, located at river km 56, in 1988 and 1992. During these analyses five 1.0 m^2 quadrats were sampled. The hand removal of clams from quadrats, as was used throughout this study, probably missed small individuals (<25 mm), and thus underestimated density. However, all collections throughout the study were conducted by the same technique and therefore reflect real changes in the population. Air temperature data were obtained from the United States Department of Commerce (1969 - 1990).

RESULTS

ENVIRONMENTAL HISTORY AND DISTRIBUTION

The occurrence of *Rangia cuneata* in the Neches River is probably very recent and can be traced with records of development of the Sabine-Neches deep water navigation channel, salt water encroachment up the river, and industrialization along the river. Kane (1959), in a study of late Pleistocene and Recent sediments, faunas, and geomorphology developed a history of the Sabine Lake-Sabine Pass area, into which the Neches River flows and where the river's parent population of *Rangia* had its origin (Fig. 1). Kane (1959) found whole shells and fragments of *R. cuneata* shells in sediments and cores from the northern and central regions of Sabine Lake and reefs of *Crassostrea virginica* (Gmelin) in the southern region. However, no salt water encroachment occurred up the Neches River prior to the deepening, widening, and shortening of the natural channel (Lower Neches Valley Authority (LNVA), 1961; U. S. Army Corps of Engineers, 1981). Thus, *R. cuneata* could not have existed in the river until development of the deep water navigation channel from the Gulf of Mexico to Beaumont, which allowed salt water encroachment and extended the distribution of *Rangia* from Sabine Lake up the Neches River (Fig. 1). Cain (1975) reported that *Rangia* larvae could be carried upstream by passive transport or by selectively swimming in the more saline water associated with flood tides.

The earliest navigation project in the Sabine-Neches system was completed in 1878 when a 3.05 m deep cut was made through the outer bank in the Gulf of Mexico (U. S.

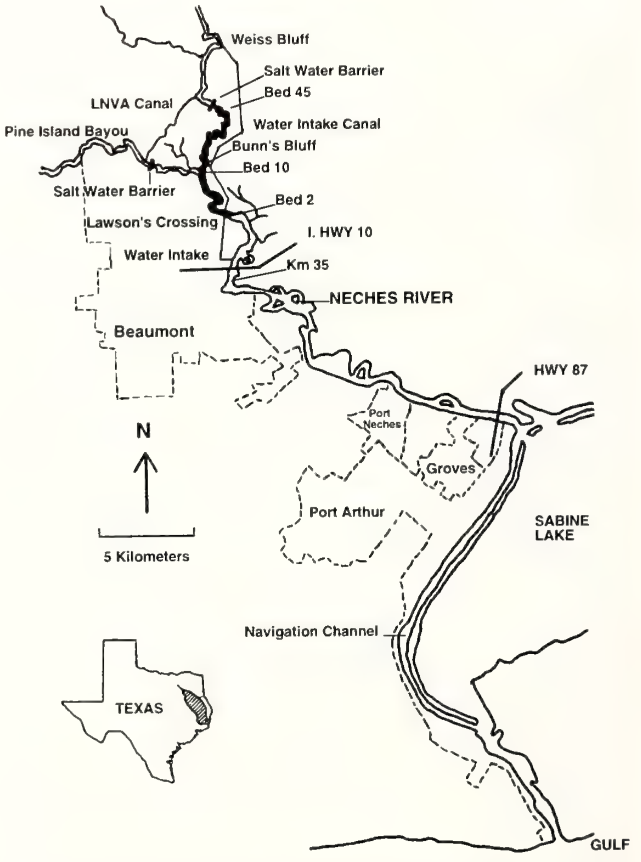

Fig. 1. Sabine-Neches estuary with locations of selected *Rangia cuneata* beds. Darkened section of Neches River channel is location of live beds.

Army Corps of Engineers, 1981). By 1900 a 7.6 m deep channel had been cut along the west bank of Sabine Lake to Port Arthur. At this time forestry, lumber milling, and rice farming were the most important features of the area economy, and navigation up the Neches River by deep-draft vessels was seasonal (U. S. Army Corps of Engineers, 1981).

In 1901, the Spindletop oil field was discovered and the trend toward oil refining and related industries spurred enlargement of existing waterways. In 1907 a 3.05 m deep channel was completed to the mouth of the Neches River and in 1914 a 7.6 m deep channel was completed to Beaumont (present day river km 35). At this time, salt water encroachment first became a problem and several pump stations on the lower river, which pumped water for irrigation of rice, had to be abandoned [Lower Neches Valley Authority (LNVA), 1961]. Also, in 1914 the Beaumont municipal water intake located at river km 36 had to be abandoned and a new intake was constructed at Lawson's Crossing (river km 41.6). In 1915 the water intake was extended upriver to Bunn's Bluff (river km 48.8) and in 1927 the city was forced to extend its canal and water intake upriver to Wiess Bluff (river km 66.7) (Fig. 1) (LNVA, 1961).

During 1924-1929 a 9.1 m deep channel was constructed to Beaumont and in 1926 the LNVA Lakeview Canal was constructed so that water for irrigation, industries, and municipalities along the lower river could be taken at river km 65.6 during periods of salt water encroachment (Fig. 1). In 1927 salt water intrusion reached the LNVA Canal and since that time, during periods of salt water intrusion, temporary sheet steel barriers have been erected across Pine Island Bayou at km 4.8 and across the river at km 60 to prevent saltwater contamination of this water supply (LNVA, 1961). Since 1932, the first year records are available, the Neches River barrier has been required during 26 years and the Pine Island Bayou barrier during 32 years. The river barrier dam diverted almost all of the flow of the river through the LNVA Canal for distribution to municipalities and industries and for irrigation of rice fields. This allowed salt water from the Gulf of Mexico and the planktonic larvae of *R. cuneata* to move up river to the Pine Island Bayou and Neches River barrier sites (Fig. 1). Additional navigation improvements that increased the frequency and duration of salt water intrusion in the river include: (1) 1937-1943 - a 10.5 m deep channel, (2) 1950 - an 11 m deep channel, (3) 1962 - a 12.2 m deep channel, and (4) 1984 - a 13.2 m deep channel (U. S. Army Corps of Engineers, 1975, 1981, 1982).

After the First World War, and especially after World War II, the petrochemical industry grew at an extremely fast rate and the lower river became grossly polluted. Most industries dumped wastes into the river without treatment turning the water black, and oil slicks degraded the shoreline (Patrick *et al.*, 1992). Whenever the salt water barrier dams were in place, salt water from the Gulf and waste effluents from the many industries along the lower river moved up to the barriers, and tidal action flushed the salt-wastewater back and forth, causing it to become more concentrated the longer the barriers were in place (Harrel, 1975; Harrel *et al.*, 1976). During many years the barriers were in place for as long as six months and the resulting pollution killed all but the most tolerant fish and invertebrates trapped below the barriers. Consequently, by 1951, the *Rangia* population in the Neches River was restricted to areas between river km 40.5 and river km 60, the saltwater barrier site (S. H. Hopkins, pers. comm., 1968). Although the upriver population had been subjected to low dissolved oxygen concentrations (<2.0 mg/1) for long time periods, it seemed to thrive (Harrel, 1975; Harrel *et al.*, 1976; Harrel and Hall, 1991).

Living *Rangia* beds had also existed in the lower river, as indicated by the presence of *Rangia* shells in the channels of the old meanders that were cut through when the navigation channel was straightened and in dredge spoils from early navigation projects. These beds were probably eliminated by dredging and toxic pollutants. Intensive surveys of this section of the river conducted by the Texas Department of Water Resources during 1969-1973 (Warshaw, 1974) and 1980 (Davis, 1984) reported 19 and 22, respectively, priority pollutants in water, sediments, or tissues at significant concentrations. These included heavy metals, phenols and cresols, polycylic aromatic hydrocarbons, phthalate esters, and general inorganics.

In 1968, when pollution abatement first began in the Neches River, the permitted biochemical oxygen demand (BOD) waste load for this section of the river was 123, 125 kg/d (220,000 lb/d), discharged primarily from oil refineries, petrochemical plants, and a large paper mill (Davis, 1984; Twidwell, 1986). The Texas Water Commission ranked the tidal Neches River as the second most polluted waterway in the state (Warshaw, 1974). Studies conducted on the tidal Neches from 1967 through 1972 examined the effects of wastewater and salt water intrusion on water quality and community structure of the macrobenthos (Harrel, 1975; Harrel et al., 1976). The results of these studies confirmed the above distribution of *Rangia*, and 45 living *Rangia* beds were located between river km 40.5 and km 57.6 (Fig. 1). An additional 19 *Rangia* beds were located in the lower 4.8 km of Pine Island Bayou, but are not included in this analysis.

In the early 1970s Federal and State regulatory agencies required all industries along the Neches estuary to upgrade their wastewater treatment systems to at least secondary treatment (U. S. Environmental Protection Agency, 1980). Since then, all wastewater treatment plants have been improved and two large regional treatment plants have been constructed. The permitted BOD waste load has been reduced 96%, to 8,717 kg/d (19,217 lb/d). Many non-BOD contributing wastes, such as heavy metals and inorganic suspended solids, were also greatly reduced. In 1986 the tidal Neches was ranked 48 of 311 classified segments (Twidwell, 1986). Harrel and Hall (1991) reported on water quality and macrobenthic community structure at the same seven collection sites before (1971-1972) and after (1984-1985) pollution abatement in the Neches River estuary. Evidence of improved water quality after pollution abatement included: (1) an increase in the annual number of taxa collected from 50 to 104, (2) minimum densities in 1984-1985 exceeding maximum densities for 1971-1972 at most stations, and (3) patterns of species dominance, Sorenson's similarity index, and Shannon's diversity index. Patrick *et al.* (1992) used the Neches River estuary for their evaluation of environmental laws on surface water quality.

During their 1984-1985 study Harrel and Hall (1991) found young *Rangia*, less than one year old, at five collecting stations located between river km 4.8 and river km 40.5. However, no mature *Rangia* have become established along the navigation channel in the lower river. This could be due to maintenance dredging of the navigation channel and frequent oil and chemical spills in this section of the river. In 1990 a bed of mature *Rangia* was located at river km 39.2, above the navigation channel, and the size of the clams indicated that this bed had been established for at least seven or eight years. During 1971 many shells but no living clams were present at this location.

DENSITY AND SIZE

During 1971, the density of the 45 live *Rangia* beds located in the Neches River varied from 16 to 665 clams/m^2 and mean density was 238/m^2. There was no correlation between density and distance upriver (r = 0.213; p = 0.078) (Fig. 2). However, mean shell length of clams significantly increased with distance upriver (r = 0.827; p = 0.0001) and lower variance occurred above Pine Island Bayou (river km 48) (Fig. 3). Ladd (1951), Gunter (1961), and Pfitzenmeyer and Drobeck (1964) reported that specimens of *R. cuneata* in fresher waters were larger than those from more saline waters, but gave no explanation. The smallest clam collected from the quadrats was 23 mm long and the largest clam was 74 mm long. The age of these specimens would be a little over one year and about 14 years, using the von Bertalanffy growth curve of Wolf and Petteway (1968). The correlation coefficient between bed density and mean clam length indicated a weak relationship (r = -0.331; p = 0.012).

The size of individual beds ranged from 42 square meters for Bed 19 at river km 53.4 to 27,360 square meters for Bed 6 at river km 44. Larger beds and higher variance were found below Pine Island Bayou, and the correlation coefficient between bed size and river km was -0.347 (p = 0.009) (Fig. 4). The boundaries of individual beds were delineated by depths greater than 1.5 m, a change in substratum from mixed substratum (sand, silty clay, and detritus) to pure substratum (sand or clay), or sunken logs, barges, or boat docks. The total area of all 45 beds was 113,115 m^2 (11.3 hectares).

Density and size data are reported for *Rangia* at Bed 2, located at river km 40.5, for 1951 from Hopkins (1970) and Hopkins and Andrews (1970) and by this investigator for 1969 to 1992 (Table 1). Hopkins (1970) and Hopkins and Andrews (1970), using data collected in 1951 and data collected by this investigator in 1969, reported that the length-frequency and density were remarkably similar and

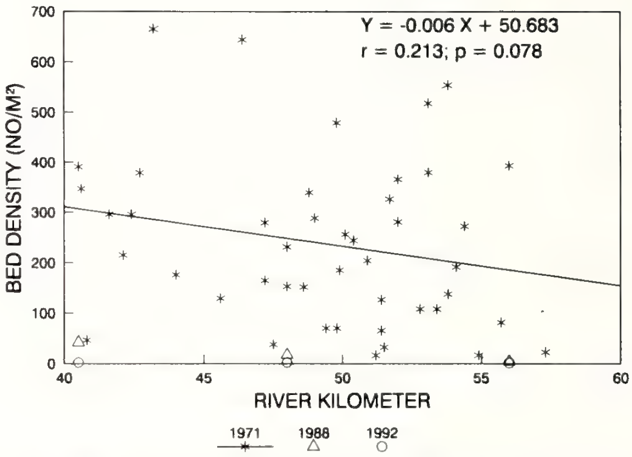

Fig. 2. *Rangia cuneata* density versus river kilometer in 1971 with best fit line, and at Beds 2, 10, and 45 in 1988 and 1992.

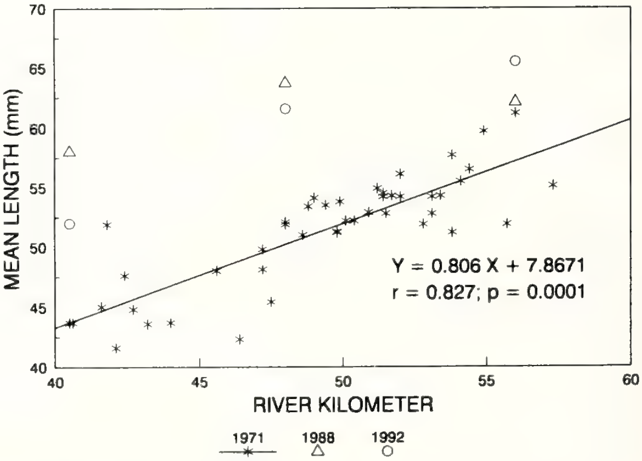

Fig. 3. *Rangia cuneata* mean shell length versus river kilometer in 1971 with best fit line, and at Beds 2, 10, and 45 in 1988 and 1992.

Table 1. Mean shell length, length extremes, and density of *Rangia cuneata* at Bed 2 in the Neches River from 1951 to 1992.

Year	Mean Length (mm)	Length Range (mm)	Density (No./m2)
1951[a]	42	37 - 56	>250
1969	45	35 - 55	496
1971	44	23 - 61	391
1977	55	46 - 67	48
1978	58	34 - 67	43
1981	56	40 - 73	92
1982	53	40 - 65	141
1983	57	36 - 69	142
1984	56	40 - 67	15
1985	59	40 - 70	23
1986	58	40 - 74	22
1987	60	32 - 72	26
1988	58	45 - 69	42
1989	61	49 - 71	34
1990	59	43 - 70	2
1991	59	54 - 64	<1
1992	52	39 - 62	2

a = Data from Hopkins (1970) and Hopkins and Andrews (1970)

that the mean age of clams from both collections was between three and four years (Table 1). Hopkins (1970) reported that the density was >250 clams/m2 during both years; although the calculated density using the 1969 data was actually 496/m2.

Between 1969 and 1992 the mean length of clams at Bed 2 increased (r = 0.745; p = 0.0006) and density decreased (r = -0.836; p = 0.0001) (Table 1; Fig. 5). The correlation coefficient between mean shell length and bed density was -0.87 (p = 0.001). Data collected in 1988 and 1992 at Bed 10, located at river km 48, and Bed 45, at river km 56, indicated that these trends were occurring at all *Rangia* beds along the river (Fig. 2 and 3).

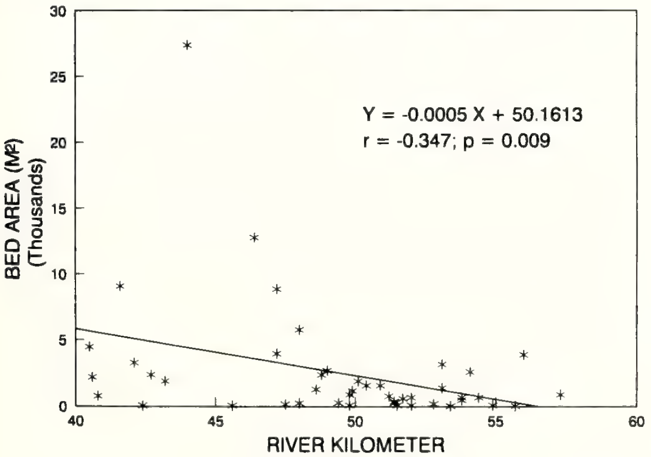

Fig. 4. *Rangia cuneata* bed size versus river kilometer in 1971 with best fit line.

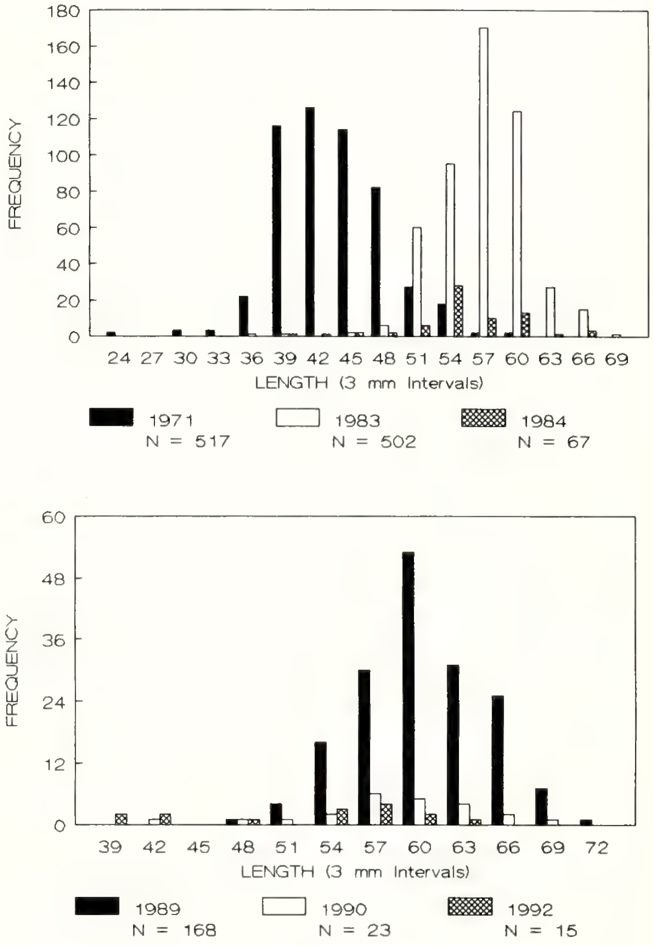

Fig. 5. Length-frequency histograms of *Rangia cuneata* at Bed 2.

The decrease in density was not constant and consisted of three years with large decreases in density (1971, 1983, and 1989) followed by several years with slight increases in density (Table 1). The sharp decreases in density between 1983-1984 and 1989-1990 resulted from high *Rangia* mortality following extreme cold fronts that occurred during December, 1983 and December, 1989. During both of these cold fronts ice formed along the shoreline and about 2 m of previously submerged shoreline was exposed due to north winds, resulting in low water levels. Two weeks after these cold fronts, the only living *Rangia* found were in water one meter or more deep, near the outer boundary of the bed where a two meter drop-off occurred. All size classes or ages of clams were affected by the cold, but the most abundant size classes had the highest mortality. The size range remained similar following both die-offs (Fig. 5). During the 1983 and 1989 cold fronts, 113 and 94 continuous hours of below freezing temperatures occurred, and new low temperature records were set (U. S. Department of Commerce, 1983 and 1989). The Texas Parks and Wildlife Department reported cold water mortalities of fish, shrimp, and crabs in many bays, coastal lakes, and estuaries along the entire Texas coast during both cold fronts. Similar cold fronts occurred during January, 1973 and January, 1976 (U. S. Department of Commerce, 1973 and 1976) and could have caused the large decrease in density between 1971 and 1977 (Table 1). However, the destructiveness of colds waves to organisms is explicable on the basis of acclimatization and depends more upon the rapidity of the temperature drop and the health of the organisms than the low temperature attained (Gunter and Hildebrand, 1951). Hopkins *et al.* (1973) reported that *Rangia* had a lower condition index (ratio of meat wet weight/internal shell volume) and meat glycogen content during November and December. This condition and time correlates with the period of major Fall spawning or cytolysis of unspent gametes, and could be the most stressful period of the year to *Rangia*. Gallagher and Wells (1969) reported a winter mortality of *R. cuneata* in the Elk River, Maryland, which is near the northernmost geographic range of the species. These are the first documented winter mortalities of *Rangia* in a Gulf of Mexico estuary.

DISCUSSION

The increase in size of clams with increasing distance upriver as occurred in 1971 (Fig. 3) and the increase in clam size at Bed 2 from 1969 through 1992 (Table 1) may be explained in terms of energy allocations for growth, reproduction, and survival during stressful times as discussed by Begon *et al.* (1990). Clams located farther downriver were more frequently subjected to salinity fluctuations that induce spawning, resulting in less energy being available for somatic growth that is beneficial for survival during stressful times. Thus, clams farther downriver would be smaller and have a shorter longevity. Likewise, clams located farther upriver could go several years without spawning, and consequently more energy can be used for growth and production of somatic biomass that could be beneficial during stressful periods and increase longevity. However, this would decrease recruitment into the population and result in a gradual increase in size and decrease in density as aging and mortalities occurred.

River discharge pattern, which effects the frequency and duration of salt water intrusion in the river, has had a profound impact on *R. cuneata* in the Neches River. Between 1951 and 1971 salt water intrusion occurred every year but one and the Pine Island Bayou salt water barrier was erected every year except 1968. The Neches River barrier was erected during 17 years of this 20 year time period. Since 1972, the Pine Island Bayou barrier was required during eight years, but only once since 1981. The Neches River barrier has been required six times since 1972, most recently in 1982. White and Perret (1974) reported that regulated river discharge from Toledo Bend Reservoir on the Sabine River had caused very low summer salinities in Sabine Lake. Freshwater flow into the Neches River estuary is controlled by releases from Sam Rayburn and Steinhagen Reservoirs, located upriver, which allow increased river discharge during summer months. Also, demands for diversion of water from the Neches River by the LNVA for irrigation of rice fields have decreased. Since 1972 the area of rice fields irrigated decreased from more than 24,281 hectares (60,000 acres) to less than 12,140 hectares (30,000 acres). Thus, time periods of salt water intrusion necessary to induce spawning of *Rangia* and suitable salinity for survival of larvae in the river have been very infrequent and of short duration during the last 20 years. The lack of recruitment and natural and cold weather mortalities have resulted in the loss of many *Rangia* beds that existed in 1971 and low densities (<1 to 2 clams/m^2) and an increased average size or age of clams at all surviving beds.

If the river discharge and cold weather trends of the past 20 years continue, *Rangia cuneata* could disappear from the Neches River. However, as pointed out by Hopkins and Andrews (1971), *R. cuneata* is a very resilient species and suitable conditions for a few years could restore the population to its former level. Also, if the third round of the U. S. Environmental Protections Agency's National Pollution Discharge Elimination System (NPDES) permit system, which began in 1987, is successful and eliminates toxic pollutants from surface waters *R. cuneata* could again become established in the lower Neches River.

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Research Note

Two common European viviparid species hybridize

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Abstract: During a morphological/electrophoretic study on the European Viviparidae, a hybrid but fertile female specimen [*Viviparus contectus* (Millet, 1813) x *V. viviparus* (Linnaeus, 1758)] was found in the Niepolomice Forest, South Poland. The specimen showed intermediate characters in its shell, anatomy, and embryonic shell. Polyacrylamide gel electrophoresis of that specimen confirmed its hybrid origin, which was marked in eight enzyme systems: specific homozygotes in both species along with a typical heterozygote in the hybrid. Interspecific differences in allozyme pattern, with different alleles in at least one locus in most enzyme systems studied, seem to indicate that *V. contectus* and *V. viviparus* are very old species, and their isolating mechanisms preventing hybridization could have become not efficient enough after such a long time since the speciation event. This is all the more probable, now that they occur sympatrically very rarely.

Viviparus contectus (Millet, 1813) and *V. viviparus* (Linnaeus, 1758) are widely distributed and common in Central Europe. However, their diagnostic characters are labile (Falniowski, 1989, 1990). In particular, this concerns shell characters, in which the presence of the umbilicus (which can be partly covered but is always visible) in *V. contectus* contrary to its absence in *V. viviparus* seems the most constant difference. Falniowski (1990: Plate iii, phot. 16-19) presented photographs of shell intermediates of the two species. On the other hand, those intermediates were undoubtedly determined anatomically as *V. contectus*. The only anatomical difference between the two species has been found in the female reproductive organs (Falniowski, 1989, figs. 45-52, also Falniowski, 1990, fig. 362A, B). In *V. contectus* the duct of the receptaculum seminis is usually narrow while leaving the receptaculum, whereas in *V. viviparus* it is strongly (rather strongly) widened; at the duct section parallel to the receptaculum, in *V. contectus* there commonly (not always) is a bulbous widening, which is absent in *V. viviparus.*

In the literature, one can find numerous opinions on ecological vicariance of the two species (e.g. Zhadin, 1928). In fact, the distribution pattern of the two species in Poland is slightly different from the one described by Zhadin (1928), but the species rarely occur sympatrically (Falniowski, 1989).

In 1976, a giant female of *Viviparus* (Fig. 1) was found in Drwinka River in Niepolomice Forest (about 30 km E from Kraków, Southern Poland). The shell measured 55 x 42 mm (normally, in *V. contectus* and *V. viviparus* it does not exceed 45 x 36 mm and 40 x 28 mm, respectively). The specimen was identified (based on shell characters alone; anatomical differences had not been known until then) as *V. contectus f. hungaricus* Hazay, 1881 (Falniowski, 1989). The shell, although more similar to *V. contectus* than to *V. viviparus*, was certainly not typical of *V. contectus*, and resembled the shell of the Danube *V. acerosus* (Bourguignat, 1862).

The weakness of diagnostic characters within the family Viviparidae is as already mentioned above, and relationships and taxonomy within the group are poorly understood. The species are described solely upon a basis of shell characters and no further study has confirmed their distinctness, although viviparids are often used as laboratory animals in various studies. Such are the reasons for starting morphological and electrophoretic studies (Table 1) on the European representatives of the family. Until now, we have already found constant differences in numerous enzyme systems among *Viviparus contectus, V. viviparus* and *V. acerosus* (Table 2), coupled with an extremely low proportion of polymorphic loci in the three species. The study is in progress.

Among viviparids collected from a small pond at Ispina, the Niepolomice Forest, in August 1991, we found one big specimen, the shell of which resembled the one of *Viviparus acerosus*, as well as the one collected in 1976 (Fig. 1) in the Drwinka River (the same region, one locality a couple of kilometres from the other). The pond is situated between the Vistula River and its right-bank dyke that is the north border of the Niepolomice Forest, Wislisko-Kobyle

Table 1. Application of polyacrylamide gel electrophoresis technique.

Electrophoresis: in slabs (180 x 130 x 0.7 mm) of 7.5% polyacrylamide gel in a continuous high-pH buffer system of Davis (1964).

Reservoir buffer: Tris-glycine (pH 8.3); 3 g Tris and 1.4. glycine per 1 *l* water.

Stacking gel buffer: Tris-HC1 (pH 6.8); 6 g Tris titrated to pH 6.8 with 1M HC1 in 100 ml final volume.

Resolving buffer: Tris-HC1 (pH 8.8); 36.3 g Tris and 48 ml 1M HC1 mixed and diluted to 100 ml final volume.

Acrylamide-bisacrylamide solution: 30 g acrylamide and 0.8 g bisacrylamide diluted to 100 ml final volume and filtered.

Stacking gel: 2.5 ml acrylamide-bisacrylamide solution, 5 ml stacking gel buffer, 2.5 ml 0.004% riboflavin, 10 ml water and 0.015 TEMED mixed and photopolymerized.

Resolving gel: (7.5%): 15 ml acrylamide-bisacrylamide solution, 7.5 ml resolving gel buffer, 39.5 ml water and 0.03 ml TEMED polymerized with 3 ml 1.5% ammonium persulfate as the catalyst.

Rns: Fourteen samples, 20 µl each, applied for a slab. Typically, a current 20-30 mA maintained for about 4 hrs until a marker dye (bromophenol blue) passed all the slab.

Reserve. The pond is about 200 m long and 50 m wide; its depth does not exceed about 2 m; there is water in the pond all year round. The shores are sandy, while the deeper parts are muddy. Along the shores, some scarce aquatic plants can be found. Besides the acerosus-like specimen, only *V. viviparus* were found occurring in mass along the shore.

There is another, small pond, situated about 500 m down the river from the one described above. Its distance from the dyke is the same as that of the former pond, but its length and width are smaller by half. Its character is also quite different: the depth is less than 1 m; the vegetation is rich, and there is no mud. The small pond temporarily desiccates. It is inhabited by a dense population of *Viviparus contectus*. Although the shells of *V. contectus* at this site are small and show some characters, in which they resemble *V. viviparus*, they are typical *V. contectus*, both anatomically and electrophoretically. The two ponds are temporarily linked by floods, which makes gene flow possible.

The big, acerosus-like specimen had the shell 44.0 mm high and 33.8 mm broad. The umbilicus was a cross between the ones of *Viviparus contectus* and *V. viviparus*, while the shell colouration with distinct bands resembled rather the latter species. Also the operculum showed intermediate characters. The specimen was a female. The receptaculum seminis with its duct (Fig. 2) resembled more the one typical of *V. viviparus*, but its diagnostic characters were intermediate enough to make determination hardly possible. There were as many as 32 embryos in the brood pouch, which is a number typical of the Polish viviparids, especially of *V. contectus* (Falniowski, 1989). From among the embryos, 17 were in early stages, with no shell; eight had small shells; seven were ready to be born. The maximum shell dimension of the embryos in the latter group was 4.4 - 5.0 mm; the shell height was up to 4.2 mm. The shells had a covered umbilicus (like in *V. viviparus*), and a blunt apex (but sharper than in *V. viviparus*). There were two rows of vestigial bristles along the body whorl. Similar

Table 2. Enzyme systems showing constant differences (no allele in common in at least one locus) between *Viviparus contectus* and *V. viviparus*, and typical heterozygotic bands in the hybrid specimen.

Enzyme name	Enzyme E.C. number	staining after
1. ß-hydroxybutyrate dehydrogenase	E.C. 1.1.1.30	Wurzinger (1979)
2. Phosphoglucomutase	E.C. 2.7.5.1	Wurzinger (1979)
3. Leucine aminopeptidase	E.C. 3.4.11.1	Rudolph and Burch (1987)
4. Lactate dehydrogenase	E.C. 1.1.1.27	Richardson *et al.* (1986)
5. Malate dehydrogenase	E.C. 1.1.1.37	Wurzinger (1979)
6. Phosphohexose isomerase	E.C. 5.3.1.9	Wurzinger (1979)
7. Hexokinase	E.C. 2.7.1.1	Richardson *et al.* (1986)
8. Adenylate kinase	E.C. 2.7.4.3	Richardson *et al.* (1986)

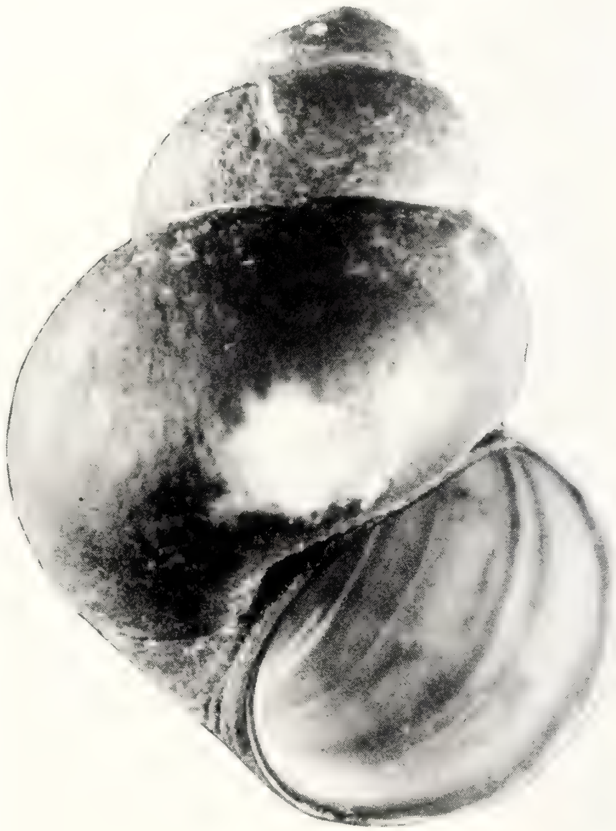

Fig. 1. *Viviparus contectus f. hungaricus* Hazay, 1881, from the Drwinka River, Niepolomice Forest (after Falniowski, 1989, plate II, phot. 9), specimen in the collection of the Zoological Museum of Jagiellonian University, Kraków. MZUJF00217.

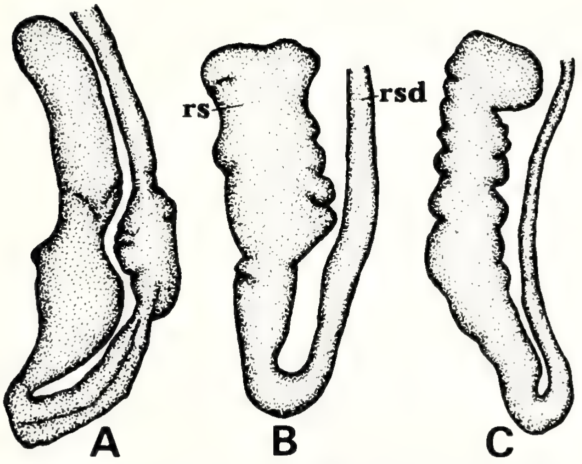

Fig. 2. Diagnostic characters in viviparid female reproductive system: receptaculum seminis (rs) with its duct (rsd): A, *Viviparus contectus;* B, the hybrid specimen; C, *Viviparus viviparus.*

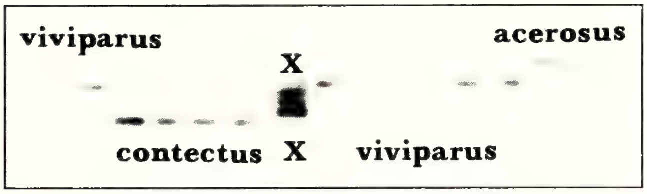

Fig. 3. Zymogram of ß-hydroxybutyrate dehydrogenase of *Viviparus viviparus, V. contectus, V. acerosus* and the hybrid specimen (marked with two "X").

bristles but longer are characteristic of young *V. contectus*, whereas young *V. viviparus* have no bristles at all.

Polyacrylamide gel electrophoresis (Table 1) of the hepato-pancreas tissue of this curious specimen revealed its hybrid character *(Viviparius contectus* x *V. viviparus)*, which was detected at eight loci of eight different enzymes (Table 2, Figs. 3, 4). At the same time, no similarity in allozyme pattern was found between the specimen and *V. acerosus.* ß-hydroxybutyrate dehydrogenase (Fig. 3) provides a good example, with specific homozygotes in each species, and a typical heterozygote in the hybrid specimen.

The above data look interesting, but their more profound interpretation requires a better understanding of viviparid relationships. It seems that *Viviparus viviparus* and *V. contectus* can produce fertile hybrids in natural conditions. Such hybrids are not common: among about 150 specimens collected at the same locality in May 1992, no such shell was found. However, the hybrid origin of the specimen presented in figure 1 is very likely. It is also not sure that the hybridization of the two species has always to lead to such heterosis. Hence, only an electrophoretical study on rich material from the Niepolomice Forest can give exact data on hybrid frequencies. Such a study is planned.

The observed interspecific differences in allozyme pattern, different alleles being found in at least one locus in almost any enzyme system studied, seem to indicate that *Viviparus contectus* and *V. viviparus* are very old species

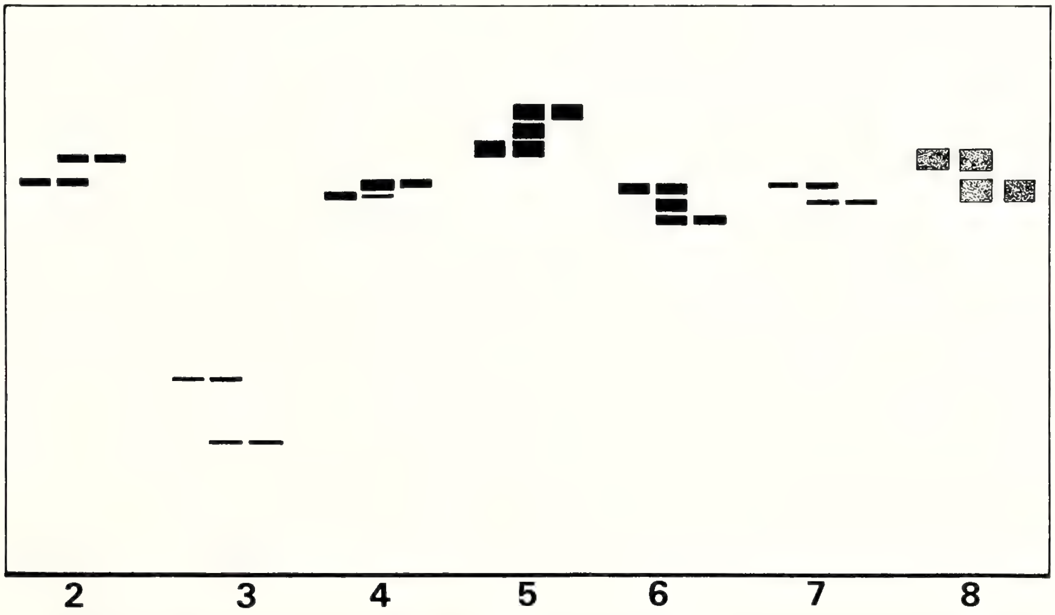

Fig. 4. Schematical diagram of isozyme electrophoretic patterns obseved in *Viviparus viviparus, V. contectus*, and the hybride individual Only these zones (presumable loci) are presented, which show no allele shared by the two species. For each enzyme system, the heterozygotic hybride specimen is in the middle, *V. viviparus* in the left, and *V. contectus* in the right. Numbers of enzyme systems as in Table 2 (2, the slower of two activity zones; 3, the fastest of several zones detected; 4, the faster of two zones; 8, one of several zones detected).

and the isolating mechanisms that prevent their hybridization could have broken down after such a long time since the speciation event (the case discussed by Wiley, 1981) which is the more probable, now that they occur sympatrically very rarely.

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Sententia

The Archaeogastropoda
A clade, a grade or what else?[1]

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Abstract: The classic concept of Thiele's Archaeogastropoda includes the Docoglossa (now Patellogastropoda), Neritacea (now Neritimorpha), Cocculinacea (now Cocculiniformia), Zeugobranchia and Trochacea (now Vetigastropoda). The recent discovery of many new archaeogastropod groups mainly from deep waters, and in particular from the hydrothermal vent habitat, necessitates a reevaluation of the taxon. Archaeogastropoda can still be clearly defined by protoconch characters and by the diagnostic streptoneurous and hypoathroid nervous system (close association of pleural and pedal ganglia). This definition also includes the Neritimorpha and the architaenioglossate groups. The amount of convergence is very high among archaeogastropods, most characters of advanced gastropods occurred several times in parallel in evolution.

As in Thiele's time, the taxon "Archaeogastropoda" is regarded as the basic gastropod stem group and should be classified as a paraphyletic taxon. Whether this stem group gave rise to a single or two lines of higher gastropods is still a matter of debate.

The taxon Archaeogastropoda was introduced by Thiele (1925) and cemented by the author in his famous "Handbuch der Systematischen Weichtierkunde" (Thiele, 1929). Five subgroups were included, namely the "Stirps" Zeugobranchia (those with two gills, now included in Vetigastropoda), the Patellacea or Docoglossa (now also called Patellogastropoda), the Trochacea (now included in Vetigastropoda), the Neritacea (now Neritimorpha), and the Cocculinacea (now Cocculiniformia). Although quite weakly defined - there was not a single diagnostic character given - the use and value of the taxon Archaeogastropoda has not been seriously questioned until very recent times [see Hickman (1988) for detailed historical review].

The first reason to question the use of Archaeogastropoda is due to the many recent discoveries of new archaeogastropod species and groups from the deep-sea, in particular but not exclusively from the strange habitat of the hydrothermal vents. Starting with the enigmatic *Neomphalus fretterae* McLean, 1981, these now include several groups, for which various ranks between genus and order have been proposed (e.g. Hickman, 1984; Marshall, 1988; McLean, 1988, 1989a, b, 1990a, b, 1992; Warén and Bouchet, 1989; Warén, 1989, 1991, 1992; Beck, 1992a, b). Anatomical investigations of these forms (e.g. Fretter, 1988, 1989, 1990; Haszprunar, 1989a, b) as well as of other long-named archaeogastropods such as the Cocculiniformia [see Haszprunar (1988a, b) for review, also 1992c] show that at least certain archaeogastropods are by far more advanced and more variable than previously thought. Obviously the assumption is no longer valid that Archaeogastropoda describes a specific level of organization, as it may be holophyletic, paraphyletic or polyphyletic. Consequently, the question arises: "What is an archaeogastropod?" or better: "Is it possible to define a taxon Archaeogastropoda and what status has that taxon?"

A second reason to question the validity of the taxon Archaeogastropoda is based on the cladistic point of view. Most cladists argue to use in phylogenetic systems only monophyletic (*sensu stricto,* i.e. holophyletic), i.e. groups with a common ancestor, which include all descendents of that ancestor (e.g. Hennig, 1966; Wiley, 1981). Because most authors regard Archaeogastropoda in the sense of Thiele (1929) as a paraphyletic (e.g. Haszprunar, 1988b; see also below) or even as a polyphyletic (e.g. Hickman, 1988), the taxon should no longer be used any more according to that view. In contrast, the author (Haszprunar, 1986, 1988b) has argued to retain paraphyletic taxa in classifications, if (and only if) (1) they are qualified as such and (2) the relationships between taxa are expressed exactly.

In this paper various characters, which have been used to define the taxon Archaeogastropoda, or which are considered primitive for gastropods in general, will be analyzed with respect to homology questions and distribution.

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[1] This contribution was provided as part of the 1992 AMU Symposium on Advances in Gastropod Phylogeny.

After that the status and validity of the taxon Archaeogastropoda will be discussed.

HOW TO DEFINE ARCHAEOGASTROPODA? – CHARACTER ANALYSIS

GENERAL REMARKS

In the following, "Archaeogastropoda" is used in the sense of Haszprunar (1988b), including the Patellogastropoda (i.e, Docoglossa, including the Neolepetopsidae, the former "hot-vent group C"), Cocculiniformia, Neritimorpha, *Melanodrymia,* Peltospiroidea (formerly "hot-vent group A"), Neomphaloidea, Vetigastropoda (including also the Seguenzioidea, see below), and the architaenioglossate groups (Cyclophoroidea, Ampullarioidea). Fossil groups could be added, if shell characters suggest their archaeogastropod nature (see below).

The term "character analysis" is used here in the sense that homology questions as well as distribution patterns are discussed. To a certain extent this has been done already earlier (Haszprunar, 1988b), nevertheless I think it is justified to present an updated review: Firstly, there are several new groups to be considered, secondly, certain characters (e.g. heterostrophy) have been differently interpreted by other authors, and finally, certain new characters (e.g. developmental timing) have been proposed meanwhile.

TELEOCONCH

It is obvious that shell shape cannot be used to define Archaeogastropoda, because all types of shell morphology are found. However, so-called "symmetrical" limpets, which do not show any coiling of the juvenile teleoconch, are not found in any other gastropod group. Confusion of symmetrical limpets with the neopilinids (Monoplacophora) can be ruled out if (1) the shell apex is posterior; or (2) a deformed protoconch is present (see below); or (3) muscle scars are visible; or (4) shell structure is considered. The presence of nacre is restricted to the archaeogastropod grade (among Gastropoda), although many groups have lost or replaced it secondarily.

Whereas a shell slit/hole(s) is characteristic for zeugobranch groups (Scissurelloidea, Fissurelloidea, Haliotioidea, and Pleurotomarioidea), it is not diagnostic at all, since shell slits are also found in Siliquariidae (Cerithioidea) and many Bellerophontida, the gastropod nature of which is still questionable [see Haszprunar (1988b) for recent review].

PROTOCONCH

Scanning electron microscopy has revealed many new characters useful for gastropod systematics. In particular, protoconch features (Fig. 1) are very useful to define distinct groups. According to the information available, four types of protoconch formation are typical for archaeogastropods:

(1) In the Patellogastropoda, the embryonic shell (i.e. protoconch I, mineralized at once by the shell gland) is usually not really coiled but more or less bent [e.g. Bandel, 1982 (figures labeled as *Cocculina reticulata* Verrill, 1884 (p. 35, Abb. 26; Tafel 8, Figs. 4, 5, 9) and *Cocculina* cf. *spinigera* (p. 36, Abb. 27A; Tafel 8, Figs. 3, 6, 8) very probably show lepetids rather than cocculinids. Compare with SEM-photos of cocculinid limpets in Marshall (1986); Warén, 1988; Fig. 1A]. Depending on the amount of yolk the embryonic shell may or may not be symmetrical (see Bandel, 1982). After metamorphosis the embryonic shell is lost together with the early teleoconch after the formation of a distinct septum leaving a characteristic scar (Smith, 1935; Bandel, 1982; Warén, 1988). Very often the axes of the embryonic and adult patellogastropod shell form a characteristic angle (e.g. Thompson, 1912). This angle has been interpreted as reminiscent of a coiled ancestor by Lindberg (1988). In this case [but see contrary arguments in Haszprunar (1988b: 370-372)], such an ancestor probably had an hyperstrophic rather than an orthostrophic teleoconch, (see legend of Fig. 1 for definitions) judging from the orientation of the axes.

(2) In the lepetelloid limpets (Choristellidae show a vetigastropod-like protoconch, see below) the apex of the embryonic shell is fused in a very characteristic way with the teleoconch, resulting in lateral pouches (cf. Marshall, 1986; Fig. 1B).

(3) The neritimorph condition (Fig. 1C) is unique among the archaeogastropods in showing a true, multispiral larval shell (i.e. protoconch II, formed and mineralized successively by the mantle margin). As outlined by Bandel (1982, 1992) this type of larval shell is diagnostic for the Neritimorpha and can be used to infer close relationships between this group and the extinct Platyceratoidea.

(4) The majority of archaeogastropods show the so-called "trochoid" condition, in which the embryonic shell is immediately followed by the teleoconch. The morphology of the embryonic shell is highly variable (e.g. Hickman, 1992: fig.5; Fig. 1D,E,F) and could well be used to diagnose minor taxa. In contrast, caenogastropods have orthostrophic larval shells (Fig. 1G-H), and heterobranchs show hyperstrophic larval shells (Fig. 1I-K), although the condition may be cryptic in the case of lecithotrophic development.

Recently, Hadfield and Strathmann (1990) described "hyperstrophic" protoconchs resp. "heterostrophy" (see legend of Fig. 1 for definitions of terms) of certain trochoid species (see also Hickman, 1992: fig. 5L). However, the term "heterostrophy" describes a relationship

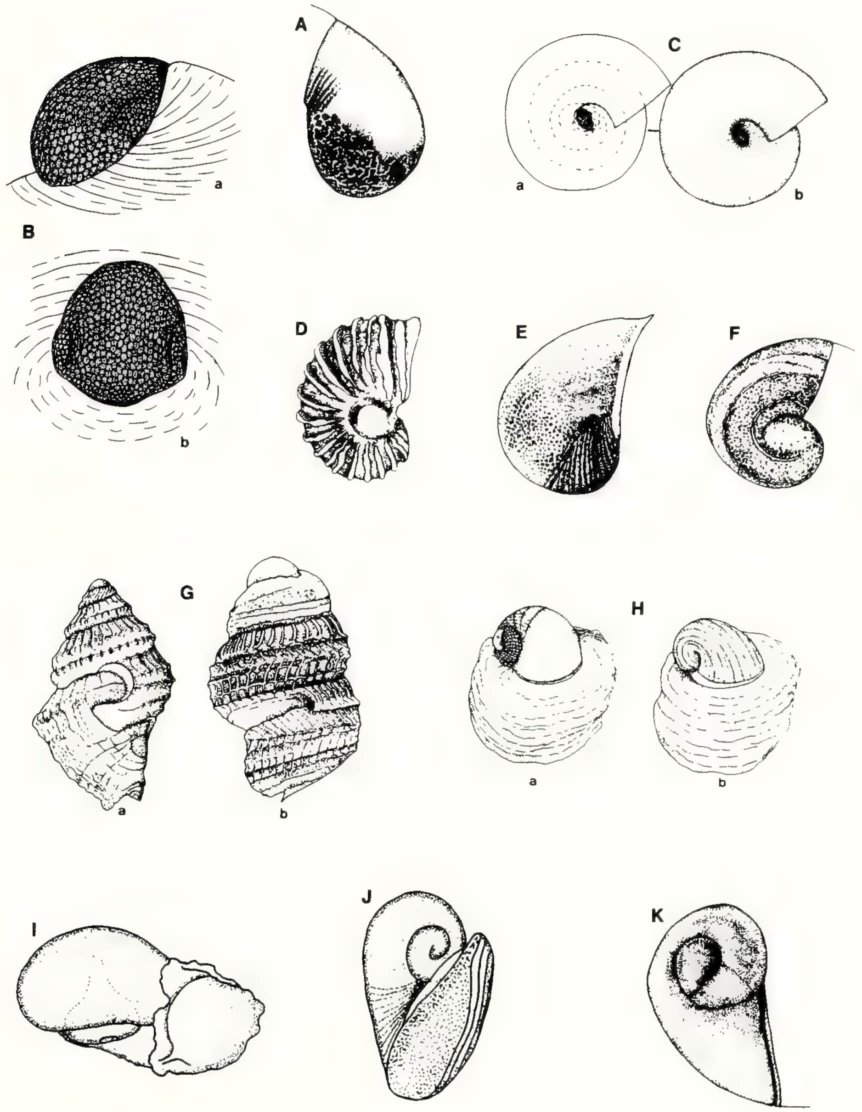

Fig. 1: Protoconchs of selected gastropods. **A.** Patellogastropoda-Lepetidae (200-800 m off SE-coast of USA). The embryonic shell (lateral view from the left) is bulbous, the deformation is not planispiral in this case (*"Cocculina reticulata"* from Bandel, 1982: fig. 26). **B**. Cocculiniformia-Pseudococculinidae: *Mesopelex zelandica* Marshall, 1986: Embryonic shell (about 135 µm wide and 210 µm long) with subreticulate sculpture from (a) lateral right and from (b) anterior showing bilateral symmetry (after SEM-photos of Marshall, 1986: figs. 10C, D). **C**. Neritimorpha-Neritidae: *Smaragdia* sp. (Red Sea): Larval shell in (a) transparent to show whorl contours, in (b) external view (from Bandel, 1982: fig 73). **D.** Vetigastropoda-Scissurellidae: *Sinezona* sp. (Gmelin, 1791) (Canary Islands): Embryonic shell with strong axial ribs (from Bandel, 1982: fig. 20). **E.** Vetigastropoda-Fissurellidae: *Fissurella angusta* Woodring, 1928: Embryonic shell with apertural ridge and sculpture caused by deformation during torsion (from Bandel, 1982: fig. 21). **F.** Vetigastropoda-Trochidae: *Microgaza vetula* L., 1767: Embryonic shell with a mixture of spiral ribs and tubercules as sculpture (from Bandel, 1982: fig. 18). **G.** Coiled Caenogastropoda: (a) *Thais haemostoma* (Muricoidea): (b) *Cerithium litteratum* (Born, 1778) (Cerithioidea): Embryonic and larval shell show different sculptures because of planktotrophic development (from Bandel, 1982: fig. 87). **H.** Caenogastropod limpets (Hipponicoidea): (a) *Hipponix conicus* (Schumacher, 18417): Embryonic and larval shell show different sculpture; (b) *Hipponix antiquatus* (L., 1767): Embryonic and larval shell cannot be distinguished by sculpture (from Bandel, 1982: fig. 82). **I.** Allogastropoda-Architectonicidae: *Philippia krebsii* (Mörch, 1875): The larval shell is hyperstrophic 1), whereas the adult shell starts orthostrophically 1). Note anastrophic 2) relationship between larval and adult shell (after Robertson, 1974 from Haszprunar, 1985b: fig. 1c). **J.** Opisthobranchia-Acteonidae: *Acteon tornatilis* L., 1758: The larval shell is hyperstrophic1), whereas the adult shell starts orthostrophically 1). Note heterostrophic (sensu stricto 2) relationship between larval and adult shell [after Thorson, (1946) from Haszprunar (1985b: fig. 1d)]. **K.** Pulmonata-Siphonariidae: *Williamia krebsii* (Mörch, 1877): The embryonic shell can be clearly distinguished from the hyperstrophic 1) larval shell (from Bandel, (1982: fig. 83).

1) "Orthostrophy" and "hyperstrophy" refer to the relationship between the orientation (left or right-handed) of a helicoid (larval or adult) shell and the orientation of the soft body. If shell and soft body are equally handed (regular gastropods, but also triphorids) this is called "orthostrophic", if they are differently handed (e.g. larval heterobranchs, neotenic Euthecosomata, also the adult ampullariid *Lanistes*), it is called "hyperstrophy".

2) "Heterostrophy" *(sensu lato)* means the different orientation of the axes of the larval and the adult shell. If the angle of axes is about 90° this is called "heterostrophy sensu stricto", if the angle is about 180° this is called "anastrophy".

between a larval shell (see Fig. 1 for definitions) and the teleoconch. In this sense it was taken by Robertson (1985), Haszprunar (1985, 1988b), Bandel (1982, 1988b, 1992), and Ponder (1991). The formation and mode of coiling of an "hyperstrophic" embryonic shell are the results of an entirely different process compared with a hyperstrophic larval shell (Bandel, 1982: 27-36; Hickman, 1992; Warén and Bouchet, 1993: 49). Therefore the "heterostrophy" of these trochoids does not corroborate the concept of heterostrophy respectively of the hyperstrophic larval shell as a basic synapomorphy of heterobranch gastropods (Robertson, 1985; Haszprunar, 1985, 1988b; Ponder, 1991). However, the presence of hyperstrophic-like embryonic shells among archaeogastropods supports the statement made by Haszprunar (1988b) that torsion and the mode of shell coiling are primarily independent features.

(5) All the above mentioned characters concern marine species. Freshwater and terrestrial gastropods generally show modifications in shell ontogeny. Whereas nearly nothing is known concerning shell ontogeny of cyclophoroids, the shell formation of ampullariids has been studied in some detail (e.g. Demian and Yousif, 1973a, b; Honegger, 1974; Lehmann, 1992). In particular Lehmann (1992) pointed out major differences between ampullariid and archaeogastropod (including neritimorph) shell development. According to his results it appears more likely that the Ampullariidae have reached the caenogastropod level concerning shell formation.

Summing up, protoconch characters enable one to distinguish clearly certain groups of (marine) archaeogastropods, caenogastropods and heterobranchs. It also shows that diagnostic features exist to define some fossil archaeogastropod groups, where protoconch data are available. This has been already applied to split up such "lumping pots" as the extinct "Euomphalacea" (e.g. Bandel, 1988a) or the recent "skeneimorphs" (e.g. Warén, 1992).

SHELL MUSCLES

As reviewed earlier (Haszprunar, 1985c, 1988b), ontogenetic as well as anatomical investigations show that in many archaeogastropods the adult shell muscles are paired, whereas they are unpaired in caenogastropods and heterobranchs. However, certain archaeogastropods also show the unpaired condition with a left muscle only (e.g. *Neomphalus*, many trochoids)

MANTLE CAVITY

The archaeogastropod mantle cavity is usually fully torted, having its opening anteriorly situated. Certain lepetelloidean limpets show a somewhat detorted orientation of the rectal-nephridial complex, whereas *Neomphalus* is unique in showing an hypertorted condition.

It is generally accepted that a paired set of pallial organs (osphradia, ctenidia, hypobranchial glands) is the primitive condition among the gastropods. Indeed, retention of this character state is found only within the archaeogastropod grade, although there are many groups that have lost one or more of the right-side organs.

CTENIDIA

As outlined elsewhere (Haszprunar, 1988b: 377-383) gastropod ctenidia are highly variable. The only gastropod gill-type, which is exclusively found within the Archaeogastropoda, is bipectinate and supplied by skeletal rods. Hickman (1988) recently proposed that this character should be diagnostic for a restricted use of "Archaeogastropoda" equivalent to Vetigastropoda. However, the same character set is found in *Neomphalus* and certain coiled peltospiroids (but not in *Melanodrymia*; see Haszprunar, 1989b), whereas on the other hand certain vetigastropods such as *Temnocinclis, Temnozaga, Fissurisepta*, many skeneids, or seguenziids) show monopectinate gills (see Cowan, 1969; Haszprunar, 1988b, 1989a, unpubl. data).

CIRCULATORY AND EXCRETORY SYSTEM

Comparable with the conditions of the pallial organs, the retention of two auricles (diotocard condition) or two kidneys is restricted to archaeogastropods. As demonstrated by the lepetodriloid and trochoid vetigastropods the loss of the right gill does not necessarily imply the loss of the right auricle. Again, however, many forms have independently reached the monotocardian or single (left) kidney condition of higher gastropods. Parallel events of loss are probable also with respect to the penetration of the pericardium by the rectum.

GENITAL SYSTEM, GAMETES, AND REPRODUCTION

Archaeogastropods are usually considered to be "primitive" with respect to reproduction in showing free (ectaquatic) fertilization. This is correlated with the so-called "primitive type" of spermatozoa, which (among gastropods) is indeed restricted to archaeogastropods. However, entaquatic (in the female's mantle cavity) or internal fertilization occurs frequently among archaeogastropods, in particular (1) in very small forms; (2) in deep-water species, including those from the hydrothermal vent habitat; (3) in freshwater or terrestrial groups. It should be stressed that in fact all so-called "advanced" conditions concerning molluscan reproduction such as internal fertilization, paraspermatozoa, spermatophores, copulatory organs, receptacula, or brooding, are found in various archaeogastropod groups. Even within the Trochoidea, developmental data (e.g. time of hatching, planktonic versus non-planktonic mode of development) vary considerably (Hickman, 1992). Concerning reproduction, Archaeogastropoda is certainly not a grouping of the same level of organization.

Recently, Jamieson (1991) pointed out for teleost fishes that the "primitive type" of spermatozoa (respectively ectaquatic fertilization) is probably an advanced feature in that group. The same conclusion has been reached for solitary ascidians (e.g. Franzén, 1992). Considering early gastropods to be very small animals (Haszprunar, 1988b, 1992a), entaquatic fertilization (by sperm of the "primitive type") could be the more primitive archaeogastropo condition.

CLEAVAGE PATTERN

Most recently Van den Biggelaar (1993) paid attention to distinct differences between archaeogastropods and higher groups (Caenogastropoda and Heterobranchia) in the spatiotemporal cleavage pattern.

(1) Whereas in archaeogastropods (*Patella vulgata* L., 1758, *Haliotis tuberculata* L., 1758 and *Gibbula magus* (L., 1767) have been investigated) the mesentoblast (i.e. the 4d—cell) is formed at the transition of the 63- into the 64-cell stage, this occurs already at the transition of the 24- into the 25-cell stage in caenogastropods (e.g. *Littorina, Crepidula, Ilyanassa*), Opisthobranchs (e.g. *Haminoea, Aplysia, Doris*), and pulmonates (e.g. *Physa, Lymnaea, Biomphalaria).* Because the formation of the mesentoblast occurs even later (72-73 cell stage) in the Polyplacophora (e.g. see Heath, 1912), the archaeogastropod condition is considered as plesiomorphic.

(2) In the gastropods there is a distinct trend to retard the formation of the first quartet cells and the formation of the prototroch not only in relation to the development of the mesentoblast, but also in relation to absolute cell numbers. In *Patella*, the trochoblasts already divide between the 32-cell and the 40-cell stage and thus clearly before the formation of the mesentoblast. In *Haliotis,* this occurs between the 52-cell and 60-cell stage; in *Gibbula,* between the 55-cell to 64-cell stage, thus nearly parallel with the formation of the mesoentoblast In caenogastropods the first division of the trochoblasts follows the formation of the mesentoblast, whereas in opisthobranchs the formation of the first quartet cells is even more retarded.

(3) The acceleration of the formation of the prototroch in caenogastropods, opisthobranchs and pulmonates is further associated with a considerably smaller number of cells, which build up the prototroch. This is probably correlated with the fact that the trochophore stage is free in *Patella,* partly free in *Haliotis* and *Gibbula,* and within the egg-capsule in higher gastropods. In the latter groups the prototroch is further transformed to the velum, which is built up by very many cells. It is unknown at present whether the trochoblasts are dividing again after differentiation or whether cells of different source are included in the velum (Van den Biggelaar, pers. comm.).

Although the present number of investigated species is still very low (e.g. no data on marine Neritoidea or allogastropods), such data on the spatiotemporal pattern of development might become very useful for phylogenetic purposes.

RADULA AND SUPPORTING STRUCTURES

The main basis of Thiele's Archaeogastropoda was the uniting of groups with a rhipidoglossate or docoglossate radula. However, the docoglossate (stereoglossate) condition, i.e. simple rasping without longitudinal bending of the radular membrane and magnetite in the lateral teeth, is likewise found in neopilinids and chitons. Moreover, the recent discovery of valvatoideans (pers. obs. on anatomy; sperm data from J.M. Healy, 1993b) with rhipidoglossate radula (but with entirely different buccal apparatus, pers. obs.), the Hyalogyrinidae (Warén and Bouchet, 1993; Warén *et al.*, 1993) omits also the second type as a simple diagnostic character for Archaeogastropoda. In addition, there are several archaeogastropod groups, in particular the Cocculiniformia (e.g. Hickman, 1983) but also several trochoid groups such as Trochaclidinae or Thysanodontinae (cf. Hickman and McLean, 1990), the radula of which do not fit any of the standard categories.

The presence of several pairs of radular cartilages is restricted to the Archaeogastropoda. Certain archaeogastropods and caenogastropods in general have a single pair or none; Heterobranchia lack true cartilages, some have secondary ones. The combination "docoglossate or rhipidoglossate radula with massive cartilages" is restricted to archaeogastropods, however.

Most archaeogastropods are provided with a so-called radular diverticulum (cf. Haszprunar, 1988: 392), which is lacking only in the architaenioglossate groups.

ALIMENTARY TRACT

As outlined elsewhere (Salvini-Plawen and Haszprunar, 1987; Haszprunar, 1988b) the presence of oesophageal pouches, which can be simply structured or papillate, is restricted to Archaeogastropoda (among Gastropoda). The same is true for the so-called "anterior loop" of the intestine. In both cases, however, certain archaeogastropods have reached independently the advanced stage.

NERVOUS SYSTEM

Pedal cords are common among archaeogastropods, but are also present in certain caenogastropods such as *Lavigeria* (Cerithioidea) (Moore, 1899 as *Nassopsis*) or in the Cypraeidae (e.g. see Riese, 1930). Therefore the character cannot be used to define Archaeogastropoda. The presence of a labial commissure is restricted to archaeogastropods, again however, many members have lost it in parallel to caenogastropods and heterobranchs.

As stated repeatedly (Salvini-Plawen and Haszprunar, 1987; Haszprunar, 1988a, b) the condition of a hypoathroid cerebropedal ring (i.e. pleural and pedal ganglia being close together) is the only character that is present in all archaeogastropods including the architaenioglossate groups. In the Viviparidae alone the hypoathroid condition is restricted to the left side, whereas the right side is epiathroid (close up of cerebral and pleural ganglia). This condition is independent of habitat (marine, freshwater, terrestrial), habit (mode of nourishment), or other modifications of the central nervous system (see above). In contrast, all caenogastropoda and primitive heterobranchs show an epiathroid condition.

The hypoathroid condition is also found in certain euthyneuran (i.e. osphradial ganglion at the right side; cf. Haszprunar, 1985b, 1988b) groups such as Aplysiomorpha or Gymnosomata (cf. Hoffmann, 1932-39) or in the Eupulmonata (Trimusculoidea, Ellobioidea, and most Stylommatophora; cf. Haszprunar and Huber (1990) for review). Therefore, I have defined the Archaeogastropoda by a "streptoneurous and hypoathroid nervous system" (Haszprunar, 1988b). Moreover, the hypoathroid-like conditions of euthyneurans differ in two fundamental aspects from that of the Archaeogastropoda:

(1) Several authors agree that in the euthyneurans the original pleural ganglion is split off into the pleural *sensu stricto* and so-called parietal ganglion (Regondaud *et al.*, 1974; Brace, 1977; Schmekel, 1985, Haszprunar, 1988b; Haszprunar and Huber, 1990). Usually the hypoathroid condition of euthyneurans concern the pleural ganglia alone, whereas the parietal ganglia are not included, but are fused with the suboesophageal or supraoesophageal ganglion.

(2) So far known the hypoathroid condition of euthyneurans is a secondary phenomenon, because during ontogeny an epiathroid condition respectively a common cerebropleural anlage is primarily established as in caenogastropods or in epiathroid heterobranchs. This is well documented in *Aplysia* (e.g. Kandel *et al.*, 1980; Jacob, 1984; Fig. 2E-F), in the Ellobiidae (Ruthensteiner, 1991, 1992; Fig. 2G-H), and in the Stylommatophora (e.g. Henchmann, 1890). In contrast, the anlage of the pleural ganglion is always close to the pedal ganglion in the Archaeogastropoda. This has been described in *Patella* (Smith, 1935), *Haliotis* (Crofts, 1937; Barlow and Truman, 1992; fig 2A-B), *Theodoxus* (Ruthensteiner, 1991: 72), *Ampullarius* (Honegger, 1974), and *Marisa* (Demian and Yousir, 1975; fig. 2C-D). The single exception is again *Viviparus* (left side hypoathroid, right side epiathroid as adults; see above), for which Andersen (1924) described a common cerebropleural anlage as in caenogastropods or heterobranchs.

Most recently, Page (1992a, b) claimed an hypoathroid condition in a dendronotoid nudibranch *Melibe leonina* (Gould, 1852). Her results are based on fine-structural studies and include: (1) the pleurals originate from a post-trochal placode as in archaeogastropods; (2) the pleurals are situated in front of the pedal ganglia; (3) the pleurals are connected to the labial lobe of the cerebral ganglia. Nevertheless, the presented interpretation causes serious problems: (1) the results are in direct contrast to all previous ones on neurogenesis in nudibranchs (e.g, Thompson, 1958, 1962; Tardy, 1970, 1974).; (2) Her "labial lobe" of pyramidellids ("sensory lobe" of Fretter and Graham, 1949) is a rhinophoral ganglion [pers. obs.; see also Haszprunar and Huber (1990) for discussion], and it is likely that the same statement can be made about the "labial lobe" of *Melibe*; (3) *Melibe leonina* (Gould, 1852) would be the only gastropod (mollusc), in which the visceral loop does not start from the pleural ganglia, but directly from the cerebral ganglia. Moreover, there is no connection between the labial lobe and the pleural ganglia in any other gastropod; (4) the "pleural" ganglia of *Melibe* strongly resemble the so-called propodal ganglia of *Onchidoris bilammelata* L., 1767, which are likewise connected with the cerebral ganglia (Chia and Koss, 1989). All these arguments suggest that the interpretation of Page (1992a, b) is incorrect. Nevertheless, modern neuroanatomical trace methods such as antibody-staining or cobalt-filling [cf. Heimer and Zaborszky (1989) for review] are necessary to finally accept or reject this proposal. However, even if the interpretation of Page (1992 a, b) would be correct, the conditions of *Melibe* are clearly not directly comparable with those of the Archaeogastropoda and do not influence the validity of the hypoathroid nervous system as a diagnostic character of the Archaeogastopoda.

SENSE ORGANS

Eyes lacking a cornea are restricted to the Archaeogastropoda, although several groups have developed closed eyes. A subradular organ is found only in certain archaeogastropods. Epipodial tentacles also occur in certain

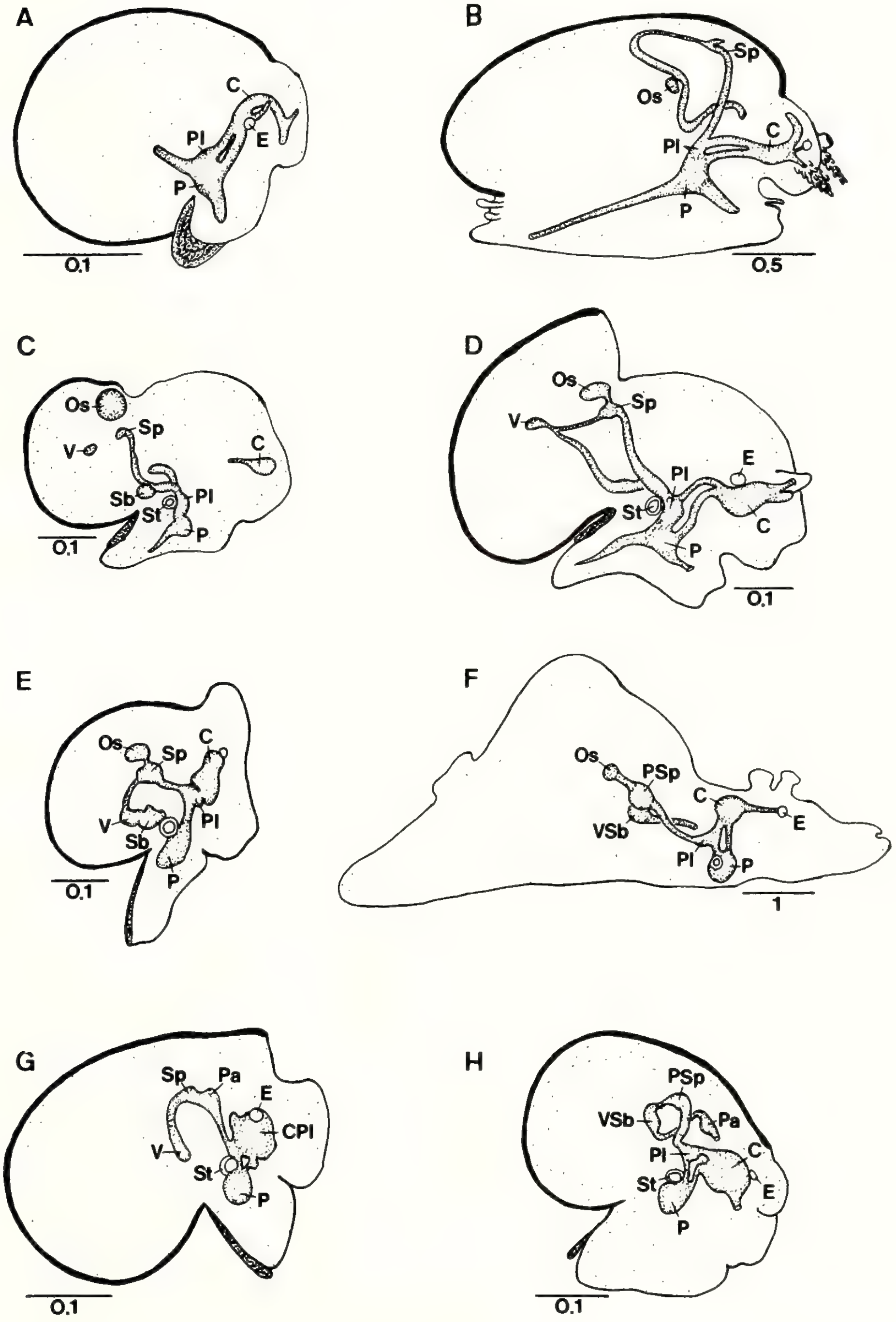

Fig. 2. Comparative view of ontogenesis of the nervous system in selected gastropods to demonstrate primary versus secondary hypoathroid conditions. Scale bars in millimeter. (C - cerebral ganglion; CPl - cerebropleural ganglion; E - eye; Os - osphradial ganglion; P - pedal ganglion, Pa - parietal ganglion; Pl - pleural ganglion; PSp - fused parietal and supraoesophageal ganglion; Sb - suboesophageal ganglion; Sp - supraoesophageal ganglion; St - Statocyst; V - visceral ganglion; VSb - fused visceral and suboesophageal ganglion). **A-B.** *Haliotis tuberculata* L., 1758 (Vetigastropoda - Haliotioidea) with hypoathroid nervous system from the beginning. A. 3 days old veliger. B. About 2 months old post-veliger (modified after Crofts, 1937). **C-D.** *Marisa cornuarietis* (L., 1758) (Architaenioglossa - Ampullarioidea) with hypoathroid nervous system from the beginning. C. Embryos stage VIII (90 hours at 25-30°C respectively 3 days at 15-20°C). D. Embryo stage X (5 days at 25-30°C respectively 14 days at 15-20°C) (modified after Demian and Yousif, 1975). **E-F.** *Aplysia californica* Cooper (Opisthobranchia - Aplysioidea): E. 3 weeks old veliger with epiathroid condition. F. 2 months old juvenile with pleural ganglion in intermediate position (adults are fully hypoathroid) (modified after Kandel *et al.*, 1979) **G-H.** *Ovatella (Myosotella) myosotis* (Draparnaud, 1804) (Pulmonata - Ellobioidea). G. Veliger 12 days old with fused cerebropleural ganglion. H. Hatchling about 21 days old with pleural ganglion in intermediate position (adults are fully hypoathroid, (modified after Ruthensteiner, 1991).

caenogastropods such as *Alaba* or *Litiopa* (Cerithioidea) (Houbrick, 1987), epipodial sense organs appear to be restricted to archaeogastropods.

So-called bursicles (Szal, 1971) have been considered to be a synapomorphy of vetigastropods (Salvini-Plawen and Haszprunar, 1987; Haszprunar, 1988b: 398-399). However, bursicles have since been found also in several lepetelloid families (Haszprunar, 1988a; unpubl.), in the enigmatic *Melanodrymia aurantiaca* Hickman, 1984 (cf. Haszprunar, 1989b), and in the seguenziids (Haszprunar, unpubl.). Whereas the latter can be reasonably included within the vetigastropods, lepetelloids and *Melanodrymia* are still considered as outgroups. Up to now, bursicles have not been reported from any caenogastropod or heterobranch.

SUMMARY OF CHARACTER ANALYSIS

Summing up, the diagnosis of "an archaeogastropod" among the Gastropoda is:

- shell shape is a "symmetrical" limpet (no juvenile coiling);
- nacre is present;
- the protoconch is patellogastropod-like (lost with a part of the teleoconch by a septurn), lepetelloid (embryonic shell apex fused with teleoconch), neritimorph (several largely overlapping whorls of larval shell), or trochoid-like (marine forms only);
- the adult shell muscle(s) is(are) paired;
- both ctenidia or osphradia or hypobranchial glands are retained;
- the ctenidia are bipectinate and supported by skeletal rods;
- both auricles are retained;
- both kidneys are retained;
- the rectum runs through the pericardium;
- ectaquatic or entaquatic fertilization by the "primitive" type of spermatozoa;
- the paired mesentoblast (4d-cell) is formed between the 63-cell and 64-cell stage, the formation of the prototroch occurs before or parallel of to this event and includes many cells;
- a docoglossate or rhipidoglossate radula type with massive cartilages is present;
- a radular diverticulum is present;
- oesophageal pouches are present;
- the "anterior loop" of intestine is present;
- a labial commissure is present;
- a streptoneurous and hypoathroid nervous system is present at least at the left side (THE ONLY DIAGNOSTIC CHARACTER);
- the eyes lack a cornea;
- a subradular organ is present;
- epipodial sense organs are present;
- bursicles are present.

With the single exception of the hypoathroid nervous system all characters listed above are valid but not diagnostic, meaning that there are archaeogastropods, which do not fulfill the specific requirement (Table 1). Because most characters listed are probably plesiomorphic (see Haszprunar, 1988b for reasoning), they also describe the gastropod archaetype (stem species or HAG = Hypothetical Ancestral Gastropod). In other words, the first gastropod was by definition an archaeogastropod.

"ARCHAEOGASTROPODA" A PARAPHYLETIC TAXON

MONOPHYLY OF ARCHAEOGASTROPODA

That archaeogastropod diagnostic characters are plesiomorphic strongly suggests that Archaeogastropoda is a paraphyletic taxon. This view is supported by the fact that the architaenioglossate groups (and certain trochoids?; cf. Healy, 1990) are linked by several characters, in particular by sperm morphology (see Healy (1988) for recent review), with the Caenogastropoda (Cerithioidea). If this is accepted, then the Archaeogastropoda in the given diagnosis cannot be clade. To decide between polyphyletic versus paraphyletic status the monophyly of Archaeogastropoda respectively of the Gastropoda as a whole has to be demonstrated.

Up to now very few people have doubted the holophyly (monophyly *sensu* Hennig, 1966) of the Gastropoda. The only group, for which a separation has recently been proposed, are the Patellogastropoda (cf. Golikov and Starobogatov, 1975; Shilenko, 1977):

However, all available evidence suggests that Patellogastropoda and all remaining gastropods have a common origin. The torsion process itself (cf. Crofts, 1955) as well as its various anatomical consequences (see review in Haszprunar, 1988b: 406) are essentially identical in all cases studied. Moreover, many pecularities of the Patellogastropoda such as the symmetrical limpet shell, many shell muscle bundles, or shallow mantle cavity, are also present in the Cocculiniformia. Thus, the latter group links the Patellogastropoda with the remaining archaeogastropod groups. Finally, the shared condition of a hypoathroid nervous system, which does not depend on the torsion process, is an independent character supporting the common origin of Patellogastropoda and all remaining Gastropoda.

TABLE 1. Characters useful for a definition of Archaeogastropoda.

TAXON	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	**23**	24	25	26	27
Patellogastropoda	+	+	+	+	–	±	✱	±	–	–	+	±	+	+	+	+	±	+	+	+	+	+	+	±	+	–	–
Cocculinoidea	+	–	+	+	–	–	–	–	–	–	–	–	–	–	?	±	–	+	+	±	–	–	+	–	–	–	–
Lepetelloidea	±	–	+	±	–	–	✱	–	–	–	+	±	±	?	?	±	–	+	±	±	±	–	+	–	–	–	±
Neritimorpha	–	–	+	±	–	–	±	+	–	±	–	±	–	–	?	+	±	+	+	+	+	–	+	–	–	–	–
Melanodrymia	–	+	+	–	–	–	–	+	–	–	–	–	–	?	?	+	–	+	+	+	–	–	+	✱	–	–	+
Peltospiroidea	–	+	+	±	–	–	–	+	+	–	±	–	–	?	?	+	–	+	+	+	+	–	+	✱	+	–	–
Neomphaloidea	–	+	+	–	–	–	–	+	+	–	–	–	–	?	?	+	–	+	+	+	+	–	+	✱	–	–	–
Scissurelloidea	–	–	+	+	+	+	±	±	+	+	+	+	+	+	?	+	–	+	+	+	+	±	+	–	–	+	+
Lepetodriloidea	–	+	+	+	–	+	–	+	+	+	+	+	–	?	?	+	–	+	+	+	+	–	+	✱	–	+	+
Fissurelloidea	–	–	+	+	+	+	+	±	+	+	+	+	±	+	?	±	–	+	+	+	+	+	+	–	+	+	+
Haliotoidea	–	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	–	+	+	+	+	+	+	+	+	+	+
Pleurotomarioidea	–	+	+	–	+	+	+	+	+	+	+	+	+	+	?	+	–	+	+	+	+	+	+	✱	+	+	+
Trochoidea	–	±	+	±	–	–	±	±	+	+	+	±	±	±	+	±	–	±	+	+	+	±	+	±	±	+	+
Seguenzioidea	–	+	+	–	–	–	–	–	+	–	+	–	–	?	?	–	–	–	–	+	+	–	+	–	–	+	+
Cyclophoroidea	–	–	✱	–	–	–	–	✱	✱	–	–	–	–	–	?	–	–	–	–	–	+	–	+	–	–	–	–
Ampullarioidea	–	–	✱	–	–	–	–	–	+	–	–	–	–	–	✱	–	–	–	–	–	+	–	+	–	–	–	–
Caenogastropoda	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–	–	–	–	±	–	–	–	–	–	–
Heterobranchia	–	–	–	–	–	–	–	±	–	–	–	–	–	–	–	±	–	–	–	–	–	–	–	–	–	–	–

Characters: (1) "symmetrical" limpet; (2) nacre; (3) archaeogastropod protoconch (see text for various types); (4) paired adult shell muscle(s); (5) paired ctenidia; (6) paired osphradia; (7) paired hypobranchial glands; (8) bipectinate gills; (9) skeletal rods in gill leaflets; (10) paired auricles; (11) two kidneys; (12) rectum runs through the pericardium; (13) fertilization is ect- or entaquatic; (14) "primitive" type of spermatozoa; (15) late formation of mesoentoblast , many trochoblasts; (16) docoglossate or rhipidoglossate-like radula type; (17) three or more pairs of radular cartilages; (18) radular caecum; (19) oesophageal pouches; (20) "anterior loop" of intestine; (21) pedal cords; (22) labial commissure; (23) streptoneurous and hypoathroid nervous system (see text for hypoathroid condition in heterobranchs); (24) open eyes; (25) subradular organ; (26) epipodial sense organs; (27) bursicles. Legend of characters: (+) present; (–) absent; (±) both conditions are present within the taxon; (✱) no relevant data; (?) no data available.

MONOPHYLY OF HIGHER GASTROPODA

During recent years, general agreement has been reached in regarding the Caenogastropoda (the majority of former Mesogastropoda and the Neogastropoda) and the Heterobranchia (allogastropods and euthyneurans) as good clades. Disagreement exists, however, whether both clades have a common or a separate origin. Whereas Salvini-Plawen and Haszprunar (1987) and Haszprunar (1988b) claimed a common origin with the epiathroid nervous system as most important synapomorphy, Ponder (1991) favored an independent origin of the Heterobranchia out of the Archaeogastropoda. Also, a most recent computer-aided reanalysis of the subject (Ponder and Lindberg, 1992) is still equivocal in this respect.

Haszprunar (1988b) has proposed that the common ancestor of Caenogastropoda and the Heterobranchia probably was a large animal (centimeter-range) and showed larval planktotrophy. If so, the metatrochal ciliary bands of the veliger larva would be directly homologous in both groupings. Homology was also stated for the orthostrophic larval shell of the Caenogastropoda with the hyperstrophic larval shell of the Heterobranchia. In contrast, Ponder (1991) assumed a small (millimeter-range) heterobranch stem species with lecithotrophic development and an independent evolution of larval planktotrophy and of the larval shell in Caenogastropoda and Heterobranchia.

Several indices support the monophyletic version: (1) The lecithotrophic heterobranchs show a more or less distinct larval shell, at least their protoconchs always show more than one whorl, calling for a planktotrophic ancestor; (2) Fossil omalogyrids and orbitestellids are lecithotrophic or planktotrophic (Bandel, 1988a, 1991); (3) Both groups, Caenogastropoda and Heterobranchia (opisthobranchs were investigated) have metatrochal ciliary bands with the so-called "discoidal reticulate lamellae", a specific type of glycocalix (Bonar and Maugel, 1982). This structure is lacking in the metatrochi of bivalvian planktotrophic larvae and in "trochophore-like" planktotrophic larvae of other spiralian phyla. Unfortunately the presence or absence of discoidal reticulate lamellae could not yet be established in the planktotrophic Neritidae. Nevertheless, this highly specific and complex structure calls for direct homology of metatrochi in Caenogastropoda and Heterobranchia and thus for common origin of larval planktotrophy in both groups; (4) Also the mentioned spatio-temporal shifts in the formation of the mesentoblast and the prototroch call for a common origin; (5) Finally, "the significant number of spermiogenic features shared by Caenogastropoda and Heterobranchia suggests either that these two groups arose from a common 'archaeogastropod' source possessing these features or that heterobranchs were derived from early caenogastropds" (Healy, 1993b).

On the other hand, recent investigations on the osphradial fine-structure of *Campanile symbolicum* Iredale, 1917 (cf. Haszprunar, 1992b) have revealed that this enigmatic relict species should no longer be regarded as a link between primitive caenogastropods and heterobranchs as previously suggested (Haszprunar, 1988b), but should be classified as the earliest offshoot among the Caenogastropoda. The same conclusions has been reached independently by spermatological investigations on a related family, Plesiotrochidae (Healy, 1993a).

In addition, the discovery of primitive heterobranchs with rhipidoglossate radula (Hyalogyrinidae; see above) seem to support Ponder's (1991) view, although a distinct archaeogastropod sister-group cannot be established at present (Haszprunar, in prep.).

"ARCHAEOGASTROPODA" IN CLASSIFICATION

So far the conclusion has been reached that Archaeogastropoda is a paraphyletic taxon, from which one or two lines (Caenogastropoda and Heterobranchia) have evolved (see above). There is a long-lasting debate in systematics, whether or not paraphyletic taxa should be allowed in phylogenetic classifications (i.e. unequivocal retranslation in the basic cladogram is possible; Wiley, 1981).

Starting from the cladistic point of view (no paraphyletic groups), what would be the alternatives?: The holophyly of Patellogastropoda and of Neritimorpha is well established by synapomorphies (Haszprunar, 1988b), and certain authors even regard them as distinct orders out of Archaeogastropoda (e.g. Lindberg, 1988; Bandel, 1992). Holophyly of Cocculiniformia is more difficult to establish (Haszprunar, 1988a, b), but also this group might be excluded as an order proper. Although there is not a single autapomorphy known for a taxon Architaenioglossa, holophyly cannot be ruled out, and the taxon has a long tradition. The real problem are the remaining groups (*Melanodrymia,* Neomphaloidea, Peltospiroidea, Vetigastropoda, Seguenzioidea). To these groups several new ones such as the Pendromidae (cf. Warén, 1991; synonym Trachysmatidae Thiele, 1925) are or will be added in the near future. Such a taxon "Archaeogastropoda" is probably again a paraphyletic assemblage, and (even more serious) no distinct diagnosis can be given for a uniting taxon.

Hickman (1988) proposed to replace Vetigastropoda (zeugobranchs, Lepetodriloidea, Trochoidea, probably also Seguenzioidea due to their recently found bursicles and epipodial sense organs) by Archaeogastropoda. But if so, what to do with the remaining groups? In other words: A restricted use of Archaeogastropoda does not solve any of the above mentioned problems, but adds the major one of a lacking diagnosis. Therefore I don't think that abolishment or a restricted use of Archaeogastropoda is helpful.

Hennig (1966, 1974) mentioned two main reasons to abolish paraphyletic groups. (1) His main argument, the equal use of para- and holophyletic taxa leads to serious confusion about the basic cladogram, is still fully valid. However, already Wiley (1981) mentioned in his Rule 1: "Taxa classified without qualification are monophyletic *sensu* Hennig (1966). Non-monophyletic groups can be added, if they are clearly qualified as such". As outlined by the author (Haszprunar, 1986, 1990) a specific marking of paraphyletic groups and a general sequential arrangement of subtaxa overcomes Hennig's (1966) main argument.

Hennig's (1974) second argument, that paraphyletic groups are some kind of polyphyletic group, must be rejected: In contrast to polyphyletic taxa, paraphyletic groups have a common ancestor (are monophyletic *sensu lato*) and represent like holophyletic (monophyletic *sensu stricto*) taxa a continuous genealogical line.

The case of Archaeogastropoda also clearly demonstrates that a paraphyletic group is not by definition defined by a "lack of x" characters, but by positive characters, which are nevertheless plesiomorphic (see summary of character analysis).

The final cladistic argument, that only holophyletic taxa are "natural entities" and that paraphyletic groups are "arbitrary constructions" is rejected on following reasons: (1) Classification does not concern a group or its phylogeny itself, but a reconstruction of phylogeny, the nature of which is always hypothetical and probabilistic. According to Darwin (1872) "natural" means "strictly genealogical" (see also Wiley, 1981: rule 1); this requirement is fulfilled by the marked use of paraphyletic groups. (2) All paraphyletic groups once were holophyletic, meaning that they included all their descendents. Until the descent of Caenogastropoda and Heterobranchia "Archaeogastropoda" in the given definition was a holophyletic group.

The use of marked paraphyletic taxa has a number of additional advantages (cf. Haszprunar, 1986, 1990): (1) More stability: many traditional or even nomenclatorically conserved (genera, species) paraphyletic taxa such as "Archaeogastropoda" can be still used in a phylogenetic system, if they are clearly marked. (2) So-called "chronospecies" such as (+) *"Homo erectus"* can be expressed unequivocally and clearly distinguished from offshoots such as (+) *Homo sapiens neanderthalensis.* (3) Combination of Wiley's (1981) *sedis mutabilis* and the marking of paraphyletic taxa enables clear expression of so-called "metataxa" (cf. Gauthier, 1986: i.e, holo- or paraphyletic) such as in the case of "Architaenioglossa" with Ampullarioidea and Cyclophoroidea both with *sedis mutabilis* (*s.* Haszprunar, 1988b).

In the case of "Archaeogastropoda" an additional argument can be made in favor of its marked retention: there are numerous species and groups, extinct or recent (e.g. Pendromidae or *Adeuomphalus and Palazzia;* cf. Warén, 1991), where conchological or radular or morphological evidence clearly allows their inclusion among the archaeogastropods in the given definition, but where classification within one of the subgroups cannot yet be established. Retaining "Archaeogastropoda" as a formal taxon allows a much clearer defined "pot" for such forms.

Summing up, I recommend the retention of "Archaeogastropoda" as a formal taxon in gastropod classification (cf. Haszprunar, 1988b). The given definition, which is mainly based on protoconch and neural characters, is valid for most extinct and recent forms. However, as expressed by its marking: have in mind that "Archaeogastropoda" is not a clade but a paraphyletic taxon. In fact, "Archaeogastropoda" is the stem group of the Gastropoda, yet it shows the widest secondary radiation of all gastropod groups.

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Giving and receiving: the tropical Atlantic as donor and recipient region for invading species

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Abstract: After the middle Pliocene uplift of the Central American seaway (3.1 to 3.6 million years ago), the western Atlantic fauna became isolated from that of the eastern Pacific, but connections with the tropical Indo-West-Pacific and eastern Atlantic were maintained. By analyzing the distibution, fossil record, and relationships of shallow-water shell-bearing molluscs (those living in less than 100 m depth) in the western Atlantic, we ascertained the extent to which the western Atlantic has served as a recipient and as a donor region for invading taxa.

At least 33 species in the western Atlantic are late Pliocene or Pleistocene invaders from the Indo-West-Pacific (17 species) or eastern Atlantic (16 species), whereas at least 39 species dispersed eastward across the Atlantic from the Americas to West Africa. Eleven species derived from the Indo-West-Pacific are included in both tallies, because they probably first dispersed westward from the Indian Ocean around southern Africa to Brazil and the Caribbean region before spreading eastward across the Atlantic to West Africa. Most of this dispersal is probably by means of planktonic larvae, but some species could have been spread as rafting adults.

Oceanic currents and prior extinction histories determine the pattern of interchange among tropical marine biotas. Within the tropics, the western Atlantic suffered the greatest molluscan extinctions since the early Pliocene (about 60 to 70%); it is also the region in which the great majority of immigrants have become common and geographically widespread. Extinction in the eastern Atlantic, eastern Pacific, and Indo-West-Pacific has been much less, and immigrants to these regions often have restricted geographical distribution there, and could be represented by populations that are not self-sustaining.

Biogeographers working with living species have divided the biosphere into a number of provinces, each of which is characterized by species found only in that region. The often unstated assumption is that these provinces have a certain continuity and cohesiveness, and that therefore they can be treated as biologically meaningful units above the species level. A consequence of this interpretation is that biogeography has been pervaded by attempts to define boundaries between provinces and to establish criteria for recognizing a region as biogeographically distinct.

As we learn more about the phylogenetic relationships and fossil record of species, the idea of provincial purity and integrity is giving way to the realization that many geographical regions support species whose geographical origins and histories vary widely. Some evolved in the region they presently occupy, whereas others arose or evolved elsewhere. There is abundant evidence that the distributional limits of species change over the course of time. For example, if a species is initiated as a small geographical isolate, it often expands its range subsequently. Other species undergo range contractions as local populations become extinct. These considerations lead to a more dynamic view of provinces, one that admits extinctions and invasions of species. Changes in the distributional limits of species affect the distinctiveness as well as the boundaries of provinces. Instead of ascertaining where these boundaries should be drawn, we can ask to what extent regions have served as sources for invading species, as refuges for species that have contracted their ranges, and as places suitable for the successful establishment of species that originated elsewhere.

Answers to these questions require a fossil record that is biogeographically and statigraphically sufficient to trace the histories of many lineages. The Neogene record of shell-bearing molluscs, though necessarily incomplete and insufficiently known in some regions, is, nonetheless, ideal for this purpose. Coupled with cladistic and molecular studies, analyses of this record could reveal much about the dynamics of species distributions and about the integrity of biogeographical provinces.

In this paper we devote particular attention to biogeographical connections between the tropical western Atlantic and other tropical marine regions. Before mid-Pliocene time (about 3.1 to 3.6 million years ago), the Central American seaway connected the western Atlantic with the eastern Pacific, so that many species were held in common between these two regions. The connection was interrupted by the mid-Pliocene uplift of the Central American isthmus. Connections between the western Atlantic and the two other tropical marine regions, the Indo-West-Pacific and eastern Atlantic, were maintained, however. Dispersal of planktotrophic larvae and rafted adults westward or eastward across the Atlantic maintains a faunal connection between the eastern and western Atlantic (Scheltema, 1971). The link with the Indo-West-Pacific is by way of dispersal around South Africa from the southwestern Indian Ocean to the central and western Atlantic.

By analyzing the distribution, history, and relationships of western Atlantic shell-bearing molluscs, we ask two related questions in this paper. First, to what extent and by which molluscan lineages has the western Atlantic been invaded from elsewhere in the tropics during the last three million years? Second, to what extent has the western Atlantic contributed invaders to other tropical regions during the last three million years, and which lineages have taken part in this invasion?

METHODS

We have compiled data on the geographical distribution, fossil record, and relationships of shell-bearing molluscs living in the tropical western Atlantic, an area we define as extending from Cape Hatteras, North Carolina, USA, to the vicinity of Rio de Janeiro, Brazil. Our aim was to identify species that invaded either westward or eastward across the Atlantic following the mid-Pliocene uplift of the Central American isthmus. To that end, we compiled a list of all amphi-Atlantic species (those living on both sides of the Atlantic), based largely on the primary taxonomic and systematic literature. We have also relied heavily on the faunistic accounts of von Cosel (1982), for the Cape Verde Islands, and Leal (1991), on the fauna of islands and sea mounts off Brazil. Some of the purported cases of amphi-Atlantic distributions are not based on a critical comparison of eastern and western Atlantic specimens. Some of the cases we report could therefore turn out to represent pairs of closely related eastern and western Atlantic species. In his compilation of amphi-Atlantic species, Talavera (1982) included many species whose distribution on both sides of the Atlantic is clearly in error or not well documented. We have therefore chosen not to include Talavera's amphi-Atlantic records unless other sources corroborate such a distribution. Wood-boring pholadid and teredinid bivalves were also excluded.

Species were inferred to have invaded during the last three million years to the western Atlantic from elsewhere in the tropics if (1) they or their likely ancestors are unknown as fossils in the western Atlantic before mid-Pliocene time, (2) they or their ancestors have a fossil record earlier than Pliocene elsewhere in the tropics, and (3) they have no close relatives (ancestral or sister species) in the tropical eastern Pacific. The rationale for the first and second criteria is obvious, but the third criterion requires brief explanation. If a western Atlantic species has a close fossil or living relative in the eastern Pacific, we can infer that the species or its ancestor was already present in tropical America during or before mid-Pliocene time, when the Central American seaway was still open. The vast majority of western Atlantic species with close eastern Pacific relatives indeed have fossil records extending to early Pliocene and often Miocene time.

We have excluded from this analysis all species that live only in waters more than 100 m deep. As a rule, deep-water taxa are not well represented in the fossil record, so that direct historical evidence from the fossil record is often lacking. Moreover, an amphi-Atlantic distribution could reflect a continuous benthic population of adults rather than a link between eastern and western populations maintained by overwater dispersal.

Potential invaders to the western Atlantic were divided into two groups. The first is composed of species that probably came from the Indo-West-Pacific around southern Africa at a time when the coastal waters of south Africa were warmer than today. Species belonging to groups with a long fossil record in the Indo-West-Pacific but not the eastern Atlantic were assigned to this group of invaders. The second group is composed of amphi-Atlantic species whose fossil record in the eastern Atlantic extends back beyond mid-Pliocene time. Amphi-Atlantic species found only on offshore islands in either the eastern Atlantic (Cape Verde and Canary Islands, for example) or the western Atlantic (Lesser Antilles or Fernando de Noronha, for example) were distinguished from those that occur on the coasts of the continents.

The western Atlantic could have contributed species to other tropical regions since the mid-Pliocene. Potential invaders from the western to the eastern Atlantic were identified in cases where the eastern Atlantic fossil record is no older than mid-Pliocene.

Many amphi-Atlantic species do not fall into either group of invaders. Some species will have achieved their amphi-Atlantic distribution before the mid-Pliocene. Others are not well understood taxonomically, biogeographically, or paleontologically. We have compiled a list of all shallow-water shell-bearing amphi-Atlantic species but we have not attempted to trace their history of invasion.

INVADERS FROM THE INDO-WEST-PACIFIC

At least 20 western Atlantic gastropods are inferred to have arrived from the Indo-West-Pacific region since mid-Pliocene time (Appendix 1). Of these, 11 species (indicated by an asterisk) are endemic to the Atlantic but have their closest relatives in the Indo-West-Pacific. For example, the trochid *Synaptocochlea picta* of the western Atlantic is the only member of its genus in the Atlantic, and is very similar to *S. concinna* (Gould, 1845), known from the Pleistocene and Recent of the Indo-West-Pacific (see Kay and Johnson, 1987; Leal, 1991). The cassid *Casmaria atlantica* is the only Atlantic species of its genus. It is extremely similar to the Indo-West-Pacific *C. ponderosa* (Gmelin, 1791), especially to the Indian Ocean form sometimes given the name *C. cernica* (Sowerby, 1888) (see Abbott, 1968). The only eastern Pacific species of *Casmaria, C. vibexmexicanum* (Stearns, 1894), is in the *C. erinacea* (Linnaeus, 1758) species complex and is not close to either *C. atlantica* or *C. ponderosa* (Abbott, 1968). The genus *Casmaria* has a Pleistocene fossil record in the western Pacific and Indian Oceans but is not known as a fossil in the Atlantic. Gibson-Smith and Gibson-Smith (1981) tentatively suggested that *C. atlantica* arose via *Phalium (Tylocassis) cicatricosum* (Gmelin, 1791) from the New World *P. granulatum* line, which appeared during the early Miocene. They pointed to similarities in protoconch characters and in the lack of sculpture on the later teleoconch whorls. This scenario requires that the outer-lip prickles characteristic of *Casmaria* evolved independently in the Indo-West-Pacific member of this genus and in *C. atlantica.* We reject this scenario in favor of the simpler idea that *C. atlantica* is derived from an Indian Ocean form of *C. ponderosa*, which entered the Atlantic during relatively recent time. The tonnid *Eudolium crosseanum* of the Atlantic is close to the Indo-West-Pacific *E. pyriforme* Sowerby, 1914 (see Marshall, 1992). The genus *Eudolium* is known from the Oligocene onward in the eastern Atlantic and from the early and late Miocene of the eastern United States, but *E. crosseanum* and the Atlantic and Indo-West-Pacific *E. bairdii* may not have descended from these earlier forms and are themselves not known as Atlantic fossils. *Malea (Quimalea) noronhensis*, known only from islands off Brazil (Leal, 1991), is very similar to the widespread Indo-West-Pacific *Malea pyrum* (Linnaeus, 1758). It is the only New World representative of the subgenus *Quimalea.* All other fossil and living species of *Malea* in the Americas belong to the nominate subgenus (see Petuch, 1989). The genus *Tonna* is unknown as a fossil in the Americas. *T. galea* is known living in both the Atlantic and the Indo-West-Pacific region, but *T. maculosa* is endemic to the Atlantic, being closely similar to the Indo-West-Pacific *T. perdix* (Linnaeus, 1758). The ranellid *Cymatium (Septa) occidentale* is the only Atlantic representative of the *C. rubeculum* (Linnaeus, 1758) species complex of the Indo-West-Pacific (Beu, 1986). *C. (Ranularia) ridleyi* of the western Atlantic is very similar to *C. sarcostomum* (Reeve, 1844) from the Indo-West-Pacific. Among the Bursidae, the western Atlantic *Bursa natalensis* is very close to, and sometimes synonymized with, *B. latitudo* Garrard, 1961 (for a discussion see Leal, 1991). *Bursa thomae* is extremely similar to the Indo-West-Pacific *B. rhodostoma* (Sowerby, 1871). A fossil possibly related to *B. thomae* was described by Jung (1969) from the Pliocene Melajo Clay of Trinidad. *Bufonaria (Marsupina) bufo* is the only member of its genus in the Atlantic; all other members are Indo-West-Pacific in distribution. Because *B. bufo* differs at the subgeneric level from other members of *Bufonaria*, the possibility exists that this species has been in the Atlantic since before mid-Pliocene time. However, it is unknown as a fossil and has no close relatives in the eastern Pacific fauna. Finally, the architectonicid *Psilaxis krebsii* of the Atlantic is extremely close to the Indo-West-Pacific *P. oxytropis* (A. Adams, 1855). It is known fossil from the late Pliocene or early Pleistocene Bowden Formation of Jamaica (as the subspecies *lampra* Woodring, 1928) and may therefore have arrived from the Indo-West-Pacific as early as the late Pliocene (see Robertson, 1973).

Besides *Bursa thomae* and *Psilaxis krebsii*, only one other species inferred to have arrived in the Atlantic from the Indo-West-Pacific after uplift of the Central American isthmus has a fossil record in the New World. Robinson (1990) reported *Gyrineum louisae* from the early Pleistocene Moín Formation of Costa Rica.

It is possible that several Atlantic taxa with eastern Pacific counterparts also arrived in the Atlantic directly from the Indo-West-Pacific, and that they are therefore not derived from ancestors living in the New World before the closure of the Central American isthmus. Examples include the ranellids *Cymatium aquatile, C. cynocephalum, C. labiosum, C. mundum, C. muricinum, C. nicobaricum, C. parthenopeum, Charonia tritonis variegata, Linaetella caudata* (see e.g. Beu and Cernohorsky, 1986; Beu and Knudsen, 1987; Beu and Kay, 1988). The eastern Pacific representatives probably arrived in the New World from the west after uplift of the isthmus, along with numerous other species, and independently of the invasion of the same stocks to the tropical Atlantic (see Emerson, 1991). Which scenario is correct cannot be resolved with the presently available evidence, but for now we have chosen to be conservative by not including the above species as immigrants to the Atlantic directly from the Indo-West-Pacific.

The inference of invasion from the Indo-West-Pacific to the Atlantic is based in part on negative evidence, namely, the absence of a pre-Isthmian New World fossil record. Such evidence is, of course, always suspect. It is always possible that some of these species were already present in the Atlantic at the same time the Central American seaway closed. This could apply to *Bursa (Lampadopsis) grayana* (Dunker, 1862) (= *B. pacamoni* Matthews and Coelho, 1971), a species today known only from Brazil.

This bursid is very close to *B. davidboschi* Beu, 1986, from the Indian Ocean, and could have been descended from an Indo-West-Pacific population. Beu (1986), however, has recorded *B. grayana* from the early Pliocene or late Miocene Gurabo Formation of the Dominican Republic. If the species did arrive from the Indo-West-Pacific region, it could have done so well before the isthmus in Central America was uplifted and without leaving eastern Pacific relatives. It is possible that other Atlantic species whose affinities lie with Indo-West-Pacific species will also be recovered as pre-isthmian fossils in the New World. In the absence of such evidence, however, and given that there are no close relatives in the eastern Pacific, we prefer the interpretation that these Atlantic species are post-isthmian invaders from the Indo-West-Pacific.

We have not included the ranellid *Linatella succincta* in the list of invaders to the Atlantic from the Indo-West-Pacific. The species is apparently unknown as a fossil, and is closely related or identical to forms from the eastern Pacific and Indo-West-Pacific (Emerson, 1991). Within the Atlantic, the species occurs on the African coast only in Gabon (Beu and Cernohorsky, 1986). It is possible that *L. succincta* is an invader from the Indo-West-Pacific, but the evidence in favor of this conclusion is not persuasive.

Of the 20 invaders from the Indo-West-Pacific to the Atlantic (Appendix 1), 11 (55%) occur on both sides of the Atlantic (Appendix 2). Six of these 11 species, however, have extremely limited distributions in the eastern Atlantic. *Bursa ranelloides, B. thomae, Cymatium occidentale,* and *Tonna maculosa* occur in the eastern Atlantic only on offshore islands (Appendix 2), whereas *Eudolium bairdii* and *E. crosseanum* are known from only a few Mediterranean records (Marshall, 1992). This implies that these species or their ancestors came directly from the Indo-West-Pacific to the western Atlantic and subsequently dispersed to the eastern Atlantic. Further support for this interpretation comes from the fact that six of the Indo-West-Pacific immigrants or their descendants are known in the Atlantic only from the American side, and that no immigrants are limited in the Atlantic to the African side. We believe that that principal dispersal route was from the southwestern Indian Ocean around southern Africa to St. Helena and thence northward and westward to Brazil and the Caribbean Region. Such dispersal is likely only at times when southern Africa was warmer than it is today. St. Helena's marine fauna of molluscs and crustaceans is well known for the presence of taxa known otherwise only from southern Africa or the Indo-West-Pacific (E. A. Smith, 1890; Chace, 1966).

DISPERSAL ACROSS THE ATLANTIC

We recognize 123 shell-bearing molluscs as occurring in shallow waters (less than 100 m deep) on both sides of the tropical and subtropical Atlantic (Appendix 2). Of these, 108 are gastropods, 15 are bivalves, and one is a scaphopod. Eleven of the amphi-Atlantic species (all gastropods) are inferred to have arrived from the Indo-West-Pacific after the Central American seaway was closed; they were dealt with in the preceding section. Most of the remaining 113 amphi-Atlantic species or their ancestors already existed in the Atlantic basin when the Central American seaway was still open. Some of these species could already have had an amphi-Atlantic distribution at that time. At least 43 species (37 gastropods, 6 bivalves) are inferred here to have dispersed either eastward or westward across the Atlantic following the mid-Pliocene uplift of the Central American isthmus (Tables 1-3). Of these 44 species, 28 dispersed eastward from the Americas to the coasts of Europe and West Africa, whereas 15 dispersed westward. These numbers exclude the previously discussed immigrants from the Indo-West-Pacific, which are inferred to have dispersed first westward across the south Atlantic and then secondarily eastward again to the eastern Atlantic.

A majority (22 species, 79%) of the 28 taxa inferred to have dispersed eastward from the Americas to the African side of the Atlantic have very limited distributions in the eastern Atlantic. For example, the fissurellid keyhole limpet *Diodora cayenensis* is known in the eastern Atlantic only from the Canary Islands, whereas on the American side it is widespread (Leal, 1991). As a fossil, this species is known not only from the western Atlantic, but also from the eastern Pacific, where Schremp (1981) recorded it from the early Pliocene Imperial Formation of Southern California.

The small littorinid *Nodilittorina (Fossarilittorina) meleagris* is known in the eastern Atlantic only from Ghana (Rosewater and Vermeij, 1972; Rosewater, 1981), but in the western Atlantic it has a wide distribution. The species is unknown as a fossil, but all other species of the subgenus *Fossarilittorina* occur in the western Atlantic and eastern Pacific (Rosewater, 1981; Reid, 1989).

The calyptraeid *Crepidula (Bostrycapulus) aculeatus*, which is known in the eastern Atlantic only from the Cape Verde Islands (von Cosel, 1982), lives in both the western Atlantic and eastern Pacific. It has a fossil record in eastern North America extending back to the middle Miocene (Hoagland, 1977).

The helmet shell *Cassis tuberosa* (Cassidae) occurs in the Cape Verde Islands and nowhere else in the eastern Atlantic (von Cosel, 1982). The lineage of *C. tuberosa* was present during the early Miocene in Florida, and was represented in the eastern Pacific during the early Pliocene (Vokes, 1990). The cassid *Phalium (Tylocassis) granulatum* is also insular in the eastern Atlantic, but in the Americas the subgenus *Tylocassis* occurs in the late Miocene Gatun Formation of Panama and is represented by living species in both the western Atlantic and eastern Pacific (Abbott, 1968). Exactly the same applies to the bursids *Bursa corrugata* and *B. granularis,* the buccinid *Colubraria testacea,* and the bivalves *Arca imbricata* (Arcidae), *Arcopsis adamsi* (Noetiidae), *Dendostrea frons* (Ostreidae), and *Pseudochama radians* (Chamidae) (see Woodring, 1964, 1973; Beu, 1980; von Cosel, 1982; Leal, 1991).

A number of amphi-Atlantic species confined in the eastern Atlantic to offshore islands perhaps also have dispersed eastward from the Americas, but the evidence from the fossil record and systematic relationships is weaker. Species in this category include the hipponicids *Hipponix antiquatus* and *H. subrufus*, the naticids *Natica livida* and *Polinices lacteus*, and the ranellids *Cymatium aquatile, C. labiosum*, and *C. muricinum.* Most of these species are closely related or identical to Indo-West-Pacific as well as to eastern Pacific species, so that we cannot be sure when or in what way they achieved an amphi-Atlantic distribution. We have included them among eastward dispersers (Table 1) because there is no fossil record of these species in the eastern Atlantic. In the case of *C. labiosum*, there are late Pliocene or early Pleistocene records in the western Atlantic from the Bowden Formation of Jamaica and the Móin Formation of Costa Rica (Beu and Knudsen, 1987). *C. aquatile* is known from the Pliocene of Ecuador in the eastern Pacific (Beu and Kay, 1988).

TABLE 1. Eastward-dispersing species in the tropical Atlantic.

Diodora cayenensis
Lucapinella limatula
Cheilea equestris
Crepidula aculeata
Hipponix antiquatus
H. subrufus
Nodilittorina meleagris
Natica livida
Polinices lacteus
Bursa corrugata
B. granularis
Cymatium aquatile
C. labiosum
C. muricinum
Linatella caudata
Cassis tuberosa
Phalium granulatum
Thaisella coronata
Trachypollia nodulosa
T. turricula
Colubraria testacea
Coralliophila caribaea
Arca imbricata
Arcopsis adamsi
Nodipecten nodosus
Dendostrea frons
Pseudochama radians
Papyridea soleniformis

Only six eastward-dispersing species have broad ranges in the eastern Atlantic. *Cheilea equestris* (Calyptraeidae), the muricids *Thaisella coronata, Trachypollia nodulosa*, and *T. turricula*, and the bivalves *Nodipecten nodosus* (Pectinidae) and *Papyridea soleniformis* (Cardiidae) are widespread in West Africa as well as in the western Atlantic, and all have counterparts in the eastern Pacific.

Fossils referred to *Cheilea equestris* by Vokes (1975) from the early Miocene Chipola Formation of Florida indicate that this species has been in the western Atlantic for a very long time. It could have been derived from a species of the Eocene of Europe (Vokes, 1975). The genus *Cheilea* was present in Europe from Eocene to late Miocene (Tortonian) time, but the species *C. equestris* probably represents a secondary invasion of the eastern Atlantic from the west.

Species of *Thaisella* are known in the Americas since at least middle Miocene time. *T. coronata* is very similar or identical to *T. trinitatensis* (Guppy, 1869), which is known from the early Pliocene Cercado Formation of the Dominican Republic and still lives in the western Atlantic (Vokes, 1989). Typical *T. coronata* is also known from the western Atlantic, and has been in the eastern Atlantic since at least the Pleistocene (Rosso, 1974).

The scallop *Nodipecten nodosus* is widely if patchily distributed in the eastern Atlantic. In tropical America, *N. nodosus* can be traced back to the late Miocene (J. T. Smith,1991), but in the eastern Atlantic the species has been reported as a fossil only from the late Pleistocene of the Canary Islands (Meco Cabrera, 1982).

The cardiid bivalve *Papyridea soleniformis* is widespread in the western Atlantic but has a very patchy distribution in the eastern Atlantic, where it is known from the Cape Verde Islands and Angola (Voskuil and Onverwagt, 1989). There is a closely related eastern Pacific species, *S. aspersa* (Sowerby, 1833).

Among westward-dispersing species (Table 2), only four (27% of 15 species) have or had very limited ranges in the western Atlantic. *Cymatium kobelti* has only been recognized in the western Atlantic as a fossil from the Pliocene of Colombia (Beu and Knudsen, 1987). The only western Atlantic occurrence of *C. trigonum* is off the coast of Venezuela (Finlay and Vink, 1982). Two other species, the bursids *Bursa marginata* and *B. scrobiculator*, are represented by Miocene to Recent populations in the eastern Atlantic, but have been reported in the western Atlantic only as late Pliocene or early Pleistocene fossils in the Moín Formation of Costa Rica (D. G. Robinson, pers. comm.).

Only one other purportedly amphi-Atlantic species has a markedly limited distribution in the western Atlantic.

TABLE 2. Westward-dispersing species in the tropical Atlantic.

Littoraria angulifera
Cerithium guinaicum
Hinea lineata
Charonia lampas
Cymatium kobelti
C. trigonum
Bursa marginata
B. scrobiculator
Ranella olearia
Epitonium albidum
Pugilina morio
Pseudomalaxis zanclaeus
Spirolaxis centrifuga
Mathilda barbadensis
Siphonaria pectinata

Vasum globulum Lamarck, 1816, is reported to occur in the Lesser Antilles as well as in West Africa (see Vokes, 1966, for a review). Faber (1988), however, has pointed out that the West African records of this species are erroneous, and that *V. globulum* is a western Atlantic species closely related to the southern Caribbean *V. capitellus* (Linnaeus, 1758).

Two other western Atlantic species with a very limited range are probably derived from eastern Atlantic species in relatively recent times. *Thais nodosa meretricula* Röding, 1798, known from islands off Brazil and from Ascension Island in the central south Atlantic, is distinct from but very closely related to the West African *T. n. nodosa* (Linnaeus, 1758) (see Rosewater, 1975; Leal, 1991). There is no similar species in tropical America, either living or fossil. The littorinids *Nodilittorina vermeiji* Bandel and Kadolsky, 1982, from islands off Brazil, and *N. miliaris* (Quoy and Gaimard, 1833) from Ascension Island, are extremely similar to the west African *N. granosa* (Philippi, 1848), but have no close relatives in the Americas (see Reid, 1989; Leal, 1991). As in the case of *Vasum globulus*, we have not included these two probable western Atlantic derivatives of eastern Atlantic taxa in our tally because of the absence of a fossil record.

The other westward-dispersing species are widely distributed in the western Atlantic, but most are unknown as fossils and therefore appear to be relatively recent immigrants to the American coasts. The melongenid *Pugilina morio,* which is found in mangrove environments from the southern Caribbean to Brazil, as well as in West Africa, is unknown as a western Atlantic fossil but is reported from the Pleistocene of West Africa (Rosso, 1974). Melongenids are abundantly represented as fossils in Miocene and Pliocene formations in the western Atlantic and eastern Pacific, but none of the species resembles *P. morio* and none can be referred to the genus *Pugilina.*

The pulmonate limpet *Siphonaria (Mouretus) pectinata* is not closely related to any other western Atlantic siphonariid. Although the species has no fossil record, we interpret it as a westward disperser because it belongs to a subgenus that is otherwise known only from southern Africa and the northwestern Indian Ocean (see Hubendick, 1945, 1946). Morrison (1963) believed that *S. pectinata* was introduced by humans from West Africa, where it is abundant on rocky shores, to the western Atlantic. He pointed to the patchy distribution of the species in the Caribbean basin as evidence for this intepretation. Wave-exposed species such as *S. pectinata* are rarely susceptible to accidental human transport. Moreover, *S. pectinata* has a planktotrophic larva, which would under favorable circumstances make overwater dispersal possible. We therefore believe that *S. pectinata* dispersed from West Africa to the Americas in relatively recent times without the aid of people.

We have included the planaxid *Hinea lineata* among westward dispersers for two reasons. First, there is no fossil record of *Hinea* in tropical America, and no species of this genus occurs in the eastern Pacific (Houbrick, 1987, 1992). Second, although *Hinea* itself is not known as a fossil in the eastern Atlantic, there were middle Miocene species such as *Planaxis (Dalliella) dautzenbergi* Glibert, 1949, from the Helvetian (= Tortonian) of the Loire Basin in France, that have some features in common with *Hinea* (see Glibert, 1949). *H. lineata* is abundant and widespread on both sides of the tropical Atlantic.

Another likely recent immigrant from the east is the mangrove-associated littorinid *Littoraria (Littorinopsis) angulifera.* The subgenus *Littorinopsis* is diverse and widespread in the Indo-West-Pacific, and has existed in the eastern Atlantic since the early Eocene (Reid, 1986, 1989). It is unknown in the eastern Pacific, where the four extant mangrove periwinkles belong to the subgenera *Littoraria* s.s. and *Bulimilittorina* (see Reid, 1989). Woodring 1957) reported a small, almost completely decorticated, fossil from the early Miocene Culebra Formation of Panama as "*Littorina* sp. cf. *L. angulifera*". One of us (GJV) has examined this specimen at the U. S. National Museum of Natural History in Washington. The shell has a lower spire than do most species of *Littorinopsis*, but there are no preserved features that make distinction between *Littorinopsis* and *Littoraria s.s.* possible. The rich fossil record of the Pliocene of Florida contains several species of *Littoraria* (Petuch, 1991), but none is similar to *L. angulifera* and none belongs to the subgenus *Littorinopsis*. We therefore believe that *L. angulifera* arrived quite recently in the western Atlantic. We cannot exclude the possibility that *L. angulifera* is a late Pliocene or Pleistocene derivative of the Indo-West-Pacific *L. scabra* (Linnaeus, 1758), and that the Atlantic *L. angulifera* followed the dispersal route of other immigrants from the Indo-West-Pacific. Under this scenario, *L. angulifera* would have originated in the western Atlantic and subsequently spread to the eastern Atlantic. This would imply that *Littorinopsis* had become locally extinct in West Africa before the arrival of *L. angulifera*. We know nothing about the Pliocene and Pleistocene fossil record of *Littorinopsis* in the Old World, but the mangrove biota of West Africa is quite rich in species and does not appear to have been ravaged by extinction. We therefore favor the hypothesis that *L. angulifera* dispersed westward to the Americas from Africa, and consider less likely the more complex hypothesis that the species invaded the western Atlantic from the Indo-West-Pacific and subsequently spread to West Africa.

Three other westward-dispersing species, *Ranella olearia* (Ranellidae), *Epitonium albidum* (Epitoniidae), and *Mathilda (Fimbriatella) barbadensis* (Mathildidae), all belong to lineages with a history extending to the early Miocene or Oligocene in Europe (see Glibert, 1949; Beu, 1976, 1980; Janssen, 1978a, b). To our knowledge, they have no American fossil record, and are not close to any eastern Pacific species.

Six of the 16 species inferred to have dispersed westward across the Atlantic are known as late Pliocene or Pleistocene fossils in the Americas. Three of these (*Cymatium kobelti, Bursa marginata,* and *B. scrobiculator*) are not known living in the western Atlantic today, and were discussed above. *Spirolaxis centrifuga* (Architectonicidae) has been reported from the late Pliocene or early Pleistocene Bowden Formation of Jamaica (Bieler, 1984), and *Cerithium guinaicum* appears in the correlative Moín Formation of Costa Rica (Houbrick, 1974). The ranellid *Charonia lampas* occurs in the early Pleistocene Mare Formation of Venezuela (Beu, 1976). None of these species has close relatives in the eastern Pacific, and none can be traced back beyond the late Pliocene in the western Atlantic. The lineages of *Bursa marinata, B. schrobiculator, Charonia lampas,* and *Spirolaxis centrifuga* extend back to the Miocene in Europe (see Beu, 1970, 1980; Bieler, 1984). The phylogenetic relationships of *Cerithium guinaicum* have not been worked out, but this species is the only member of its genus in America without either close eastern Pacific relatives or clear ancestors from the Miocene or early Pliocene (see Houbrick, 1974).

GENERAL DISCUSSION

From the analysis presented in the last two sections, we infer that at least 35 shallow-water shell-bearing molluscan species in the western Atlantic are late Pliocene or later invaders from the Indo-West-Pacific or eastern Atlantic, and that at least 39 species dispersed eastward across the Atlantic during this same time interval (Table 3). Eleven species derived from the Indo-West-Pacific are included in both tallies, because they probably first dispersed westward from the Indian Ocean to the Americas and subsequently spread eastward to the tropical eastern Atlantic. The number of westward dispersers would be increased by two if we included *Nodilittorina vermeiji* and *Thais nodosa meretricula*, which are probably western Atlantic derivatives of eastern Atlantic species.

TABLE 3. Summary of invasion of molluscs to and from the tropical Atlantic following uplift of the Central American isthmus.

Category	Number of Species
Invasion to western Atlantic	
Total	35
Invaders from Indo-West-Pacific	20
Invaders from eastern Atlantic	15
Narrowly distributed invaders	6
Invasion to eastern Atlantic	
Total	39
Invaders from Indo-West-Pacific	11
From western Atlantic	28
Narrowly distributed invaders	22

Invaders comprise a small proportion of the faunas of the eastern and western Atlantic. Von Cosel (1982) estimated that the tropical eastern Atlantic molluscan fauna contains about 2220 species. The 39 post-isthmian invaders to that region therefore account for only about 2% of the fauna. No comparable estimates are available for molluscan diversity in the western Atlantic. However, Rosenberg (1993) reports that there are more than 2900 gastropod species between Cape Hatteras and Rio de Janeiro. The 35 shallow-water invaders to the western Atlantic therefore account for only 1.2% of this fauna. Locally, the contribution of invaders is higher, especially on oceanic islands. Thus, the molluscan fauna of the Cape Verde Islands comprises about 400 species (von Cosel, 1982), of which 27 (6.8%) are invaders from the west by our count. Of the 121 prosobranch gastropod species at Fernando de Noronha off Brazil (Leal, 1991), seven (5.8%) are identified by us as invaders from the Indo-West-Pacific or eastern Atlantic. This tally does not include *Nodilittorina vermeiji* or *Thais nodosa meretricula*, both of which appear to be derived from eastern Atlantic taxa.

Most of the dispersal across the Atlantic and from the Indo-West-Pacific is probably by planktonic larvae. Scheltema (1971) has documented the existence of planktonic larvae of many amphi-Atlantic species in the open ocean far from land, and has provided evidence that larvae remain competent to settle for many weeks or even months. It is possible, however, that several mangrove-associated species dispersed by rafting as adults on wood. *Littoraria angulifera, Thaisella coronata,* and *Pugilina morio* are typical of mangrove environments, and all can be found on logs as well as on living trees.

Whether dispersal is by planktonic larvae or by rafting adults, the routes of dispersal reflect the pattern of oceanic circulation in the Atlantic. In the southern Atlantic, the strongest trans-oceanic currents flow westward (Leal, 1991), whereas in the North Atlantic the strong Gulf Stream flows eastward (see also Scheltema, 1971). The fact that several invaders to the western Atlantic from the Indo-West-Pacific and eastern Atlantic are known mainly from South and Central America suggests to us that westward dispersal of these species was largely across the south Atlantic. Similarly, many eastward-dispersing species are restricted in the eastern Atlantic to the Cape Verde Islands, Canary Islands, or Mediterranean area. This, we believe, implies that eastward dispersal is chiefly a North Atlantic phenomenon.

Ocean currents provide the means for dispersal, but they are not alone in determining the pattern of invasion of species. Propagules can be brought to a potential recipient region, but if they fail to settle, thrive, and reproduce, the invasion is ephemeral. Conditions in the recipient biota must therefore be understood if we are to explain observed patterns of interchange among biotas.

The available evidence indicates that the tropical western Atlantic received approximately the same number of shallow-water immigrants (35 species) as this region exported to the eastern Atlantic (28 species). The eastern Atlantic received more species (39) than it exported (16). However, the majority of invaders to the eastern Atlantic (28 of 39 species, 72%) have extremely limited distributions in the eastern Atlantic, where they are confined either to offshore islands or to small sectors of the mainland coast. By contrast, most of the immigrants to the western Atlantic have wide ranges there; only four of the 35 species (11%) can be described as narrowly distributed in the western Atlantic. These data imply that penetration of the eastern Atlantic by immigrants has been marginal, whereas invasion of the western Atlantic has been geographically much more extensive.

The status of the eastern and western Atlantic as donor and recipient regions for invaders can be compared with that of other tropical marine regions. Since the Central American seaway closed during the middle Pliocene, the eastern Pacific has received a large number of immigrant species from the Indo-West-Pacific, especially in reef habitats (Vermeij, 1987, 1991b; Grigg and Hey, 1992). Emerson (1991) recorded 61 shell-bearing gastropods as invaders from the Indo-West-Pacific to the eastern Pacific. To our knowledge, the eastern Pacific has not exported species to other tropical regions since mid-Pliocene time. Although many of the Indo-West-Pacific immigrants are found only on offshore islands, at least 26 (46%) have penetrated to the Pacific mainland coast of the Americas. The Indo-West-Pacific has served as a donor region for many invaders to the eastern Pacific and Atlantic. We know of only one persuasive case of recent immigration to the Indo-West-Pacific from elsewhere. Lozouet (1986) has marshalled strong arguments in favor of the hypothesis that the lagoonal potamidid gastropod *Potamides conicus* Blainville, 1828, invaded the Indian Ocean from the Mediterranean during late Pliocene or Pleistocene time. It is, of course, possible that other taxa have a similar history, but detailed documentation is lacking.

The four tropical marine regions can thus be ranked according to their status as donor and recipient regions for recent molluscan immigrants. The Indo-West-Pacific has been chiefly a donor region, whereas the eastern Pacific has been only a recipient region. The eastern and western Atlantic regions fall in the middle.

These patterns of invasion could reflect the extent of prior extinction of species in the various tropical regions (Vermeij, 1991b). Among the four biotas, that of the Indo-West-Pacific probably suffered the smallest loss in overall diversity during the Pliocene and Pleistocene. Only a few taxa at the generic level disappeared from the region, although many genera and species apparently underwent contractions in range during the last three million years (Vermeij, 1986, 1991c). The western Atlantic, on the other hand, has been greatly affected by extinction. Some 60 to 70% of species and 32% of subgenera became extinct in Florida after mid-Pliocene time. Although all of this loss was compensated for, mainly by speciation, the Pliocene represents a time of very high species turnover in Florida and in other parts of the western Atlantic (see Vermeij and Petuch, 1986; Allmon *et al.*, 1993). Extinction in the eastern Pacific at the generic level was less than half that in the western Atlantic; at the species level, there was also substantial extinction, but most of the losses were compensated for by extensive speciation during the early Pleistocene, so that there may have been no net loss in diversity since the early Pliocene. No published estimates of extinction exist for the tropical eastern Atlantic, because no substantial Pliocene deposits are known from West Africa. Brébion (1979) summarized the Pliocene and Pleistocene molluscs of Morocco (now in subtropical West Africa). From his list we estimate that 21 of 87 species (24%) recorded from the Pliocene and early Pleistocene of Morocco are extinct. There are only two genera that no longer occur in the eastern Atlantic. This calculation suggests that extinction in this part of the world was much less severe than in the western Atlantic. Tropical West Africa and the tropical eastern Pacific have both been recognized as major refuges for taxa that disappeared from southwestern Europe and the western Atlantic during the Pliocene and early Pleistocene (Vermeij, 1986, 1991c).

The western Atlantic thus stands out as the region that has suffered the greatest loss of diversity during the Pliocene and Pleistocene. Although the known number of invaders in this region is small, most of the invading species have achieved wide distributions in the western Atlantic and have become common elements in the habitats they occupy. The eastern Atlantic has received a large number of immigrant species, but few have become geographically widespread and very few have become common in shallow waters. Indeed, it is not at all certain that many of the immigrant species maintain self-perpetuating populations in the eastern Atlantic. The same situation applies to the eastern Pacific. Many species have immigrated to this region, but very few have become common, and many eastern Pacific populations of Indo-West-Pacific species may be sustained only by the periodic influx of dispersing larvae from the west (see also Richmond, 1990; Emerson, 1991; Grigg and Hey, 1992). Immigration to the Indo-West-Pacific has been negligible and ecologically marginal. Thus, the greatest penetration of immigrants has occurred in the region that suffered the greatest magnitude of extinction and the greatest net loss of diversity since the Pliocene. Biotas in which the loss of diversity has been lower have been less extensively infiltrated by species invading during late Pliocene or Pleistocene time. Similar patterns have been documented for other cases of marine as well as terrestrial interchange (Vermeij, 1991a, b).

There is some evidence that patterns of invasion before the middle Pliocene were different from those later. In particular, eastward dispersal in the Atlantic may be a relatively recent phenomenon. Although systematically collected data for trans-Atlantic faunal interchange are not available for the Miocene, detailed studies of pectinid bivalves (Waller, 1991) and muricid gastropods (Vokes, 1988) indicate that many Miocene and early Pliocene taxa in tropical America owe their origins to immigration from the east. Examples include the pectinid scallop lineages of *Aequipecten mucosus* (Wood, 1828) and *Argopecten*, and the muricid lineages *"Hexaplex" brassica* (Lamarck, 1822) and *Muricanthus*. Much stronger ties link the faunas of the eastern Atlantic and tropical America during the Eocene. Dozens of genera and species occurred on both sides of the Atlantic, and may have dispersed from east to west (see e.g. Squires, 1987; Givens, 1989, 1991; Allmon, 1990). We know of no documented cases of eastward dispersal until middle Pliocene time. In the tropical Pacific, westward dispersal may also have been the rule during the early Cenozoic (Grigg and Hey, 1992). These patterns of dispersal probably reflect the predominantly westward flow of ocean currents at a time when a more or less continuous belt of tropical seaway existed at low latitudes before seaways through the Middle East, Indonesia, and Central America were constricted. Eastward dispersal in the Atlantic may have become possible when circulation in the North Atlantic (especially that in the Gulf Stream) became more vigorous during the middle Pliocene (Kaneps, 1979; Maier-Reimer *et al.*, 1990; Crowley, 1991; Crowley and North, 1991). Whether prior loss of diversity also played a role in the pattern of interchange during Miocene and earlier Cenozoic time is unknown. Our knowledge of the taxonomy and distribution of Miocene and older species is still too sketchy to permit firm conclusions to be drawn. We hope that studies of Cenozoic molluscs on a worldwide scale will be done, so that important questions about faunal interchange and extinction can be answered.

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APPENDIX 1.

List of western Atlantic species likely to have arrived from the Indo-West-Pacific region after closure of the Central American isthmus. An asterisk indicates that the species is endemic to the Atlantic but very closely related to an Indo-West-Pacific taxon; other species occur in both Atlantic and Indo-West-Pacific regions.

Gastropoda:
* *Synaptocochlea picta* (Orbigny, 1842)
* *Casmaria atlantica* Clench, 1944
* *Malea (Quimalea) noronhensis* Kempf and Matthews, 1969
Tonna galea (Linnaeus, 1758)
* *T. maculosa* (Dillwyn, 1817)
Eudolium bairdii (Verrill and Smith, 1881)
* *E. crosseanum* (Monterosato, 1869)
* *Bufonaria (Marsupina) bufo* (Bruguière, 1792)
* *Bursa (Bufonariella) natalensis* (Coelho and Matthews, 1970)
B. (Bufonariella) ranelloides (Reeve, 1844)
* *B. (Lampadopsis) thomae* (Orbigny, 1842)
Distorsio perdistorta Fulton, 1938
Cymatium (Turritriton) comptum (A. Adams, 1855)
C. (Ranularia) gallinago (Reeve, 1844)
* *C. (Septa) occidentalis* Clench and Turner, 1957
C. (Reticutriton) pfeifferianum (Reeve, 1844)
* *C. (Ranularia) ridleyi* (E. A. Smith, 1890)
C. (Turritriton) vespaceum (Lamarck, 1822)
Gyrineum louisae Lewis, 1974
* *Psilaxis krebsii* (Mörch, 1874)

APPENDIX 2.

List of shallow-water amphi-Atlantic shell-bearing molluscan species. Species occur at depths of 100 m or shallower. An asterisk indicates that there is no close eastern Pacific relative or that the fossil record of the species or its presumed ancestor does not precede the late Pliocene in the western Atlantic. Species without further annotations are known to be living on the continental coasts of both the eastern and western Atlantic. Those living in the eastern Atlantic only on offshore islands (Canary Islands, Cape Verde Islands, or Madeira) are designated "insular EA". Species known in the western Atlantic only from offshore islands are designated "insular WA". Species known in the western Atlantic only as fossils are designated "fossil WA".

Gastropoda:
Scissurella cingulata (O. G. Costa, 1861)
Diodora cayenensis (Lamarck, 1822) (insular EA)
E. tuberculosa (Libassi, 1859)
Lucapinella limatula (Reeve, 1850)
* *Littoraria (Littorinopsis) angulifera* (Lamarck, 1822)
Nodilittorina (Fossarilittorina) meleagris (Potiez and Michaud, 1838)
* *Benthonella gaza* Dall, 1889
Alaba incerta (Orbigny, 1842)
Cerithium (Thericium) atratum (Born, 1778)
* *C. (T.) guinaicum* Philippi, 1849
Fossarus ambiguus (Linnaeus, 1767)
* *Hinea lineata* (da Costa, 1778)
Crepidula (Bostrycapulus) aculeata (Gmelin, 1791) (insular EA)
Cheilea equestris (Linnaeus, 1758)
Hipponix antiquatus (Linnaeus, 1767) (insular EA)
H. subrufus (Lamarck, 1819) (insular EA)
Pedicularia sicula (Swainson, 1840)
Trivia (Dolichupis) candidula (Gaskoin, 1836)
Lamellaria perspicua (Linnaeus, 1758)
* *Gyrodes depressa* (Seguenza, 1874)
* *Natica livida* (Pfeiffer, 1840) (insular EA)
Notocochlis marochiensis (Gmelin, 1791)
Polinices lacteus (Guilding, 1834) (insular EA)
Cassis tuberosa (Linnaeus, 1758) (insular EA)
Cypraecassis testiculus (Linnaeus, 1758)
Phalium (Tylocassis) granulatum (Born, 1778) (insular EA)
Bursa (Lampadopsis) corrugata (Perry, 1811) (insular EA)
* *B. (Apsa) marginata* (Gmelin, 1791) (fossil WA)
* *B. ranelloides* (Reeve, 1844) (insular EA)
B. (Bufonariella) granularis (Röding, 1798) (insular EA)
* *B. (Bufonariella) scrobiculator* (Linnaeus, 1758) (fossil WA)
* *B. (Lampadopsis) thomae* (Orbigny, 1842) (insular EA)
* *Distorsio perdistorta* Fulton, 1938
Charonia tritonis variegata (Lamarck, 1816)
* *C. lampas* (Linnaeus, 1758)
Cymatium (Monoplex) aquatile (Reeve, 1844) (insular EA)
* *C. (Turritriton) comptum* (A. Adams, 1855)
C. (Ranularia) cynocephalum (Lamarck, 1816)
C. (Turritriton) kobelti (von Maltzan, 1884) (fossil WA)
C. (T.) labiosum (Wood, 1828) (insular EA)
C. (Monoplex) martinianum (Orbigny, 1845)
C. (Ranularia) muricinum (Röding, 1798) (insular EA)
C. (Monoplex) nicobaricum (Röding, 1798)
* *C. (Septa) occidentale* Clench and Turner, 1957 (insular EA)
C. (Monoplex) parthenopeum (von Salis, 1793)
C. (Turritriton) tenuiliratum (Lischke, 1863)
* *C. (Monoplex) trigonum* (Gmelin, 1791)
* *Gyrineum louisae* Lewis, 1974
Linatella caudata (Gmelin, 1791) (insular EA)
L. succincta (Linnaeus, 1771)
* *Ranella olearia* (Linnaeus, 1758)
* *Eudolium bairdii* (Verrill and Smith, 1881)
* *E. crosseanum* (Monterosato, 1869)
* *Tonna galea* (Linnaeus, 1758)
* *T. maculosa* Dillwyn, 1817 (insular EA)
* *Cosmotriphora melanura* (C. B. Adams, 1850)
Metaxia abruptu (Watson, 1880)
Oceanida graduata (de Folin, 1870)
Cylindriscala acus (Watson, 1883)
* *Epitonium (Hyaloscala) albidum* (Orbigny, 1842)
E. (Gyroscala) lamellosum (Lamarck, 1822)
E. striatissimum (Monterosato, 1878)
Opalia (Dentiscala) crenata (Linnaeus, 1758)
Scalenostoma subulatum (Broderip, 1832)
Cytharmorula grayi (Dall, 1889)
Stramonita haemastoma (Linnaeus, 1767)
Thaisella coronata (Lamarck, 1822)
Trachypollia nodulosa (C. B. Adams, 1845)
T. turricula (von Maltzan, 1884)
* *Typhis (Typhina) belcheri* Broderip, 1833
* *T. (Typhinellus) sowerbii* Broderip, 1833
Coralliophila caribaea Abbott, 1958 (insular EA)
C. squamosa (Bivona, 1838)
Colubraria testacea (Mörch, 1852) (insular EA)
* *Pugilina morio* (Linnaeus, 1758)
Mitrella ocellata (Gmelin, 1791)
* *Vasum globulus* Lamarck, 1816 (insular WA)
Gibberula lavalleeana (Orbigny, 1842)
Persicula interruptolineata (von Mühlfeld, 1816)
Prunum marginatum (Born, 1778)
Conus (Chelyconus) ermineus (Born, 1778)
* *Corinnaeturris leucomata* (Dall, 1881)
Drilliola loprestiana (Calcara, 1841)
Gymnobela agassizii (Verrill and Smith, 1880)
Architectonica nobilis (Röding, 1798)
Discotectonica discus (Philippi, 1844)
Heliacus bisulcatus (Orbigny, 1842)
H. cylindricus (Gmelin, 1791)
H. perrieri (Rochbrune, 1881)
Pseudotorinia architae (O. G. Costa, 1841)
* *Psilaxis krebsii* (Mörch, 1874)
* *Spirolaxis centrifuga* (Monterosato, 1890)
* *Mathilda (Fimbriatella) barbadensis* (Dall, 1889)
Eulimella scillae (Scacchi, 1835)
Pyramidella dolabrata (Linnaeus, 1758)
Hydatina physis (Linnaeus, 1758)
Micromelo undatus (Bruguière, 1792)
Philine trachyostraca (Watson, 1897)
Cylichna discus Watson, 1883
Bulla striata (Bruguière, 1792)
Atys caribaeus (Orbigny, 1842)
A. macandrewi E. A. Smith, 1872
Haminoea antillarum (Orbigny, 1841)
H. elegans (Gray, 1825)
Umbraculum umbraculum (Lightfoot, 1786)
Berthella stellata (Risso, 1826)
Pira monilis (Bruguière, 1792)
* *Siphonaria (Mouretus) pectinata* (Linnaeus, 1758)

Scaphopoda
  Dentalium striolatum Stimpson, 1851

Bivalvia
  Arca imbricata Bruguière, 1789 (insular EA)
  Arcopsis adamsi (Dall, 1886) (insular EA)
  Pinna rudis (Linnaeus, 1758)
  Lima lima (Linnaeus, 1758)
  Perna perna (Linnaeus, 1758)
  Lithophaga aristata (Dillwyn, 1817)
  Nodipecten nodosus (Linnaeus, 1758)
  Dendostrea frons (Linnaeus, 1758) (insular EA)
* *Neopycnodonte cochlear* (Poli, 1795)
* *Parahyotissa mcgintyi* Harry, 1895
  Pseudochama radians (Lamarck, 1819) (insular EA)
  Papyridea soleniformis (Bruguière, 1792)
  Gastrochaena hians (Gmelin, 1791)
  Barnea truncata (Say, 1822)
  Pholas (Thovana) campechiensis (Gmelin, 1791)

The evolution of *"Chlamys"* (Mollusca: Bivalvia: Pectinidae) in the tropical western Atlantic and eastern Pacific

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Abstract: The phylogenetic relationships and paleontological history of six species of *"Chlamys"* living in the Caribbean were analyzed for the purpose of determining how each originated and is related to geminate species elsewhere in the world ocean. Particular emphasis is on origins and dispersal relative to the closure of seaways connecting the tropical western Atlantic and eastern Pacific. The resulting systematic revision demonstrates that these species are not a monophyletic assemblage, nor are they a single genus, nor are any of them members of the genus *Chlamys* in a strict sense.

The Caribbean species *"Chlamys" multisquamata* is placed in a new genus *Laevichlamys*, which originated in the western Indo-Pacific and dispersed westward to the eastern Atlantic, thence to the western Atlantic. Arrival in the Caribbean region occurred after the mid-Pliocene seaway closure, and *L. multisquamata* has no geminate species in the eastern Pacific. True *Hinnites*, represented at present by the relic species *H. corallinus* from west Africa and by Mio-Pliocene *H. crispus* of the Mediterranean, is shown to be derived from a stem species in *Laevichlamys*.

Four of the Caribbean species, *Chlamys sentis, C. ornata, C. mildredae*, and *C. imbricata,* comprise a new monophyletic genus *Caribachlamys* characterized by a unique lecithotrophic-type larval shell. This group also originated in post-closure time, probably in the late Pliocene, and is restricted to the tropical western Atlantic. *Caribachlamys* is placed in a new tribe Crassadomini with the more plesiomorphic genus *Crassadoma.* The definition of the latter is expanded to include not only its type species, *C. gigantea* of the eastern Pacific, but also *C. multistriata* and *C. pusio* of the eastern Atlantic. The phylogenetic histories of these species are discussed and it is shown that the cemented habit of *C. gigantea* and *C. pusio* arose independently and at different times.

Lastly, *"Chlamys" benedicti* of the Caribbean is made the type species of a new genus *Spathochlamys*, which has a long history in the tropical western Atlantic but originated from ancestors in the eastern Atlantic. Entry of members of the genus into the eastern Pacific occurred via Central American seaways probably in the late Miocene, giving rise to *S. vestalis* (=*S. lowei*), which has now dispersed as far as the Gal·pagos Islands with some morphological divergence.

The results suggest that: (1) eurytopy bestows resistance to both extinction and speciation; (2) long-distance dispersal facilitates allopatric speciation but so also does lecithotrophy in reef habitats; (3) evolution within some scallop clades has been very rapid; and (4) gene flow between Bermuda and the Antilles was interrupted during the late Pleistocene. Finally, marine evolutionary events in the Neogene of the tropical Americas are related only incidentally to seaway closure; many of the differences that separate modern Caribbean and tropical eastern Pacific faunas arose both well before and well after closure.

In addition to the introduction of two new tribes, three new genera, and one new fossil species, lectotypes are designated for certain species named by Linnaeus (1758), Gmelin (1791), Poli (1795), Lamarck (1819), and Reeve (1853).

It has long been known that the modern Caribbean marine fauna was formerly part of a larger Tertiary biogeographic province that extended into the tropical eastern Pacific through connecting seaways in Central America and northern South America (Woodring, 1966). It has been assumed that the final closure of these seaways set off a divergence between the Atlantic and Pacific parts of a once continuous fauna. The Panamic fauna is said to have remained relatively unchanged, whereas the Caribbean fauna declined in diversity and species richness. These assumptions have been based mainly on data stemming from taxic censuses, particularly of gastropods at the level of genus and subgenus (Woodring, 1966; Petuch, 1982b; Jones and Hesson, 1985; Vermeij and Petuch, 1986; Vermeij, 1993; Allmon *et al.*, 1993).

New approaches, however, are yielding new information on both the timing and the effects of seaway closure. Studies of the physical stratigraphy and biostratigraphy of the Isthmus point to a final closure date of about 3.5 million years ago, in the middle Pliocene (Coates *et al.*, 1992, and references therein). Allmon *et al.* (1993) compiled species-level data on gastropods and found that the modern warm western Atlantic gastropod fauna is not less diverse than the eastern Pacific one but has undergone considerably more taxonomic turnover since closure. Budd *et al.* (1992), in a study of reef coral species, also found that taxonomic turnover, not diversity decline, was the major event in the post-closure Caribbean. Caribbean extinctions increased after closure, but so also did originations. Furthermore, these and other recent studies (Jackson *et al.*, 1993; Knowlton *et al.*, 1993; Vermeij, 1993) indicate that many of the differences that now exist between the faunas

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on the two sides of the Isthmus did not originate exactly at the time of final closure. Jackson and Jung (1992), using species-level data, found that strong contrasts between the mollusk faunas of the western Atlantic and eastern Pacific were already present 2 Ma before final closure and that extinction in the Caribbean did not become massive until 1.8 to 1.5 Ma after final closure. Collins (1992) found that the main restructuring of the benthic foraminiferal faunas of the upper continental slope to inner continental shelf of the Caribbean occurred in the latest Miocene well before seaways closed. Cheetham and Jackson (1992) concluded from a phylogenetic study of some cheilostome bryozoans that cladogenesis reached a peak in the Late Miocene "well before final closure of the Panamanian portal, but after formation of the sill that disrupted oceanic circulation patterns throughout the region." Knowlton *et al.* (1993), in a study of the biochemical and reproductive divergence of trans-isthmian pairs of snapping shrimp, found "that isolation was staggered rather than simultaneous."

It is apparent from these recent studies that species-level analyses provide new insight to the dynamics of evolutionary change in the tropical American marine faunas before and after seaway closure. Aside from a few species-level studies, however, these efforts still depend mainly on taxonomic census data, albeit at a finer level than that in previous studies.

The objective of the present paper is to examine the general question of how the Caribbean marine fauna was assembled before and after seaway closure by means of a species-level examination of phylogeny in a subset of Caribbean mollusks. Specifically, for each species considered, it will be asked where, when, and from what it originated. Are the stem groups for Caribbean species in the Caribbean or elsewhere? Is there a center of origin for Caribbean species, and how are origins distributed through time? Lastly, is there evidence for geographic subspeciation within the tropical western Atlantic? If so, what is the polarity of morphological differences among subspecies and how might this polarity be explained?

The bivalve family Pectinidae has been selected for three reasons: (1) my research concentrates on this group, and the results of earlier phylogenetic studies (Waller, 1991) can be readily applied to a new problem; (2) pectinid shells, owing to their largely calcitic composition, are commonly preserved where wholly aragonitic mollusk shells are not; (3) although Neogene pectinids appear to have low survivorship and greater extinction rates than other molluscan groups (Stanley, 1986a), they also appear to be capable of more rapid evolution and are thus ideally suited for an examination of events of the past few million years. A subset of Pectinidae consisting of species traditionally placed in the genus *Chlamys* has been selected because of their generally similar byssate life habits and alleged congeneric status. The species analyzed are the six Caribbean species of *"Chlamys"* and their close relatives elsewhere in the world ocean (Table 1). It will be shown that these species, far from being congeneric, in fact represent four extant genera distributed among three tribes. This has necessitated a taxonomic revision which has been

Table 1. Extant American *"Chlamys"* and related species of the eastern Atlantic analyzed in the present study.

Original name	Genus in this study	Tribe	Provenance	Stratigraphic range
Pecten multisquamatus Dunker, 1864	*Laevichlamys* new genus	Chlamydini	W. Atlantic & Caribbean	Pleist.-Recent
Lima gigantea Gray, 1825	*Crassadoma*	Crassadomini new tribe	E. Pacific	Lower? Mio.-Recent
Ostrea multistriata Poli, 1795	*Crassadoma*	Crassadomini	E. Atlantic & SW Indian O.	Lower Mio.-Recent
O. pusio Linnaeus, 1758	*Crassadoma*	Crassadomini	E. Atlantic	Pleist.-Recent
P. sentis Reeve, 1853	*Caribachlamys* new genus	Crassadomini	W. Atlantic & Caribbean	Plio.?-Recent
P. ornatus Lamarck, 1819	*Caribachlamys*	Crassadomini	W. Atlantic & Caribbean	Lower? Pleist.-Recent
P. (Chlamys) imbricatus mildredae Bayer, 1941	*Caribachlamys*	Crassadomini	W. Atlantic (SE Florida)	Upper Plio.?-Recent
O. imbricata Gmelin, 1791	*Caribachlamys*	Crassadomini	W. Atlantic & Caribbean	Lower? Pleist.-Recent
Chlamys benedicti Verrill and Bush, 1897	*Spathochlamys* new genus	Mimachlamydini new tribe	W. Atlantic & Caribbean	Upper? Plio.-Recent
P. (Chlamys) lowei Hertlein, 1935 [= *Pecten vestalis* Reeve, 1853]	*Spathochlamys*	Mimachlamydini	E. Pacific	Upper Mio.-Recent

extended to two eastern Atlantic species in order to establish the morphological integrity of a new tribe and to assist in the demonstration that cementation, present in one American species, is a highly polyphyletic phenomenon among pectinids.

Table 2 is a practical morphological key to the identification of the four genera listed in Table 1 plus four that are relevant to understanding phylogeny and biogeography in the tropical American regions.

MATERIALS AND METHODS

This study is based mainly on the extensive Recent and fossil shell collections of the Departments of Invertebrate Zoology and Paleobiology of the United States National Museum of Natural History, supplemented by specimens from the collection of John Waldrop and Druid Wilson, Lake Wales, Florida, the Florida Museum of Natural History Museum, Gainesville, and the Paleontological Research Institution, Ithaca, New York. Additional information stems from earlier examinations of Recent and fossil specimens housed in major natural history museums in the United States, western Europe, and Great Britain. Some new information on West Coast species was obtained after the initial version of the manuscript was reviewed. These late additions resulted from an opportunity to study collections at the United States Geological Survey office in Menlo Park, California, the Museum of Paleontology of the University of California (Berkeley), and the Los Angeles County Museum of Natural History. Morphological terms are explained in Waller (1991) and measurement definitions are given in Waller and Marincovich (1992). In accord with these earlier studies, the terms "commarginal" and "antimarginal" refer to sculptural features that are approximately parallel or perpendicular to the shell margin, respectively. In contrast, the term "radial" refers to features that radiate from the beak, meaning that these features may be nearly parallel to the margin at the disk flanks but nearly perpendicular in the midventral region.

All specimens in the Smithsonian collections have been examined with a light microscope (Wild M-5) using reflected or transmitted light, the latter particularly useful in the examination of microsculpture in thin-shelled early growth stages. Prodissoconch morphology was studied at x50 with the light microscope, with verification of inferred prodissoconch configuration provided by examination of selected specimens with a scanning electron microscope (SEM). SEM specimens were sputter-coated with gold in a vacuum chamber and examined at accelerating voltages of 10kv.

Abbreviations

AHF: Catalogue of the Alan Hancock Foundation Collection, now housed at LACM.
AM: Zoological Museum, Amsterdam.
ANSP: Academy of Natural Sciences of Philadelphia.
AOL: length of anterior outer ligament.
BMNH: The Natural History Museum, London.

Table 2. Key to some genera of *"Chlamys"* referred to in the text (asterisk (*) marks those genera that are extinct or absent in the tropical American region).

1.	Simple non-branching radial ribs introduced early and persisting throughout ontogeny	2
	Complex pattern of rib introduction, with introductions occurring through most of ontogeny	3
2.	Rib interspaces with a single medial riblet, at least in early ontogeny	4
	Rib interspaces lacking medial riblets and crossed by antimarginal, oblique, or herringbone striae; internal rib carinae limited to juvenile stage or absent	*Mimachlamys**
3.	Ribbing coarse and scaly; commarginal lirae commonly present in interspaces at least in early ontogeny; posterior margins of posterior auricles concave	6
	Ribbing fine, with repeated introductions of new ribs by medial intercalation on both valves, filling interspaces; commarginal lirae absent; posterior margins of posterior auricles convex	*Laevichlamys*
4.	Scales atop ribs concave toward dorsum; commarginals present in rib interspaces at least in early ontogeny; ribs carinate on internal shell surface near margin	5
	Scales atop ribs convex toward dorsum; commarginals in rib interspaces obscure or absent; ribs without internal carinae	*Dimarzipecten**
5.	Rib interspaces in early ontogeny crossed by more or less straight commarginal lirae	*Spathochlamys*
	Rib interspaces in early ontogeny having wavy or looped commarginal lirae of the Aequipectinine type	Genus A*
6.	Prodissoconch with short PI stage and long PII stage	7
	Prodissoconch with PI stage large and PII stage limited to a narrow fringe	*Caribachlamys*
7.	Antimarginal striae but not commarginal lirae dominant at start of ribbed stage; shagreen microsculpture sometimes present on parts of valves	*Chlamys**
	Commarginal lirae present in rib interspaces at start of ribbed stage at least on left valve; shagreen microsculpture absent	*Crassadoma*

BRM: Institut royal des Sciences naturelles de Belgique, Brussels.
CAS: California Academy of Sciences, San Francisco.
DMNH: Delaware Museum of Natural History, Wilmington, Delaware.
GNH: Museum d'Histoire naturelle de Geneve, Switzerland.
Ht.: height, the maximum dorsoventral dimension perpendicular to the hingeline.
HUB: Zoologisches Museum, Museum für Naturkunde der Humboldt Universität, Berlin.
kv: 1,000 volts.
LACM: Los Angeles County Museum of Natural History, Los Angeles, California.
LM: Rijksmuseum van Natuurlijke Historie, Leiden.
Ma: millions of years, the standard abbreviation in the Système International d'Unités of the General Conference on Weights and Measures (Harland *et al.*, 1982).
MNHN: Musèum national d'Histoire naturelle, Paris.
NMB: Naturhistorisches Museum Basel, Basel, Switzerland.
POL: length of posterior outer ligament.
PRI: Paleontological Research Institution, Ithaca, New York.
R/V: Research vessel.
SEM: scanning electron microscope or micrograph.
TU: Locality register of H.E. and E.H. Vokes, Tulane University, New Orleans.
TUI: Dipartimento di Scienze della Terra, Universita degli Studi di Torino, Torino, Italy.
UCBL: Centre des Sciences de la Terre, Université Claude Bernard Lyon I, Villeurbanne, France.
UCD: Department of Geology, University of California, Davis.
UCMP: Museum of Paleontology, University of California, Berkeley.
UF: Florida Museum of Natural History, University of Florida, Gainesville.
USFC: United States Fish Commission.
USGS: Register of Cenozoic localities of the U.S. Geological Survey.
USGS(MP): Branch of Paleontology and Stratigraphy, U.S. Geological Survey, Menlo Park, California.
USNM: Department of Invertebrate Zoology (Mollusks), National Museum of Natural History, Smithsonian Institution, Washington, D.C.
USNM(P): Department of Paleobiology, National Museum of Natural History, Smithsonian Institution, Washington, D.C.
YPM: Peabody Museum, Yale University, New Haven, Connecticut.
ZMC: Zoological Museum, University of Copenhagen, Copenhagen.

SYSTEMATICS

Family Pectinidae Wilkes, 1810 [emend. Waller, 1978]

Diagnosis.— Pectinacea having a ctenolium at least in early ontogeny.

Discussion.— Authorship of the family name is usually attributed to Rafinesque (1815). The earlier use of the name by Wilkes (1810, as "Pectinoidae") was brought to my attention by Eugene Coan (pers. comm., 1991).

The arrangement of the enormous number of living and fossil taxa of Pectinidae into a coherent phylogenetic arrangement above the species level is still far from

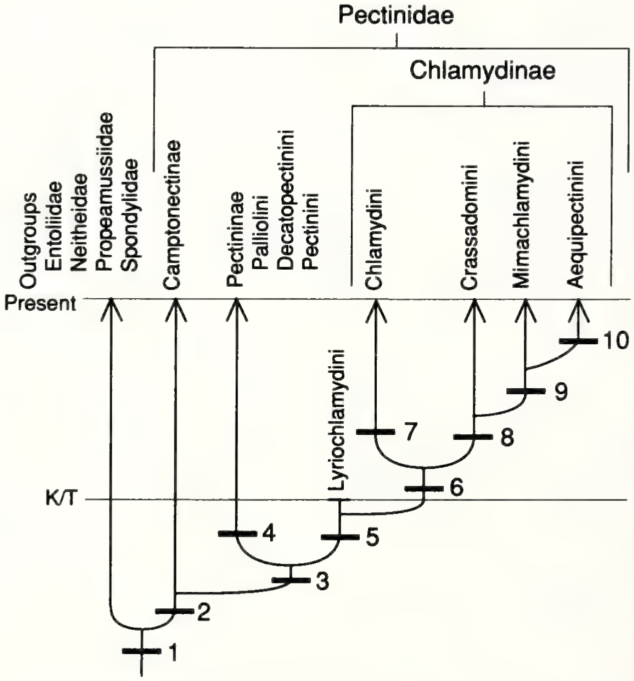

Fig. 1. A phylogeny of major groups of Pectinidae. Lineages ending in arrows are extant; the one ending at a cross-bar is extinct. K/T refers to the Cretaceous-Tertiary boundary. Numbered blocks refer to apomorphies: (1) resilium with non-fibrous core; (2) ctenolium; (3) radial plicae and straightened anterodorsal margin; (4) modified hinge teeth with dorsal and/or intermediate teeth dominant; (5) two-element hinge dentition with resilial teeth emphasized; (6) withdrawal of crossed-lamellar aragonite to inside pallial line; (7) shagreen microsculpture; (8) modified antimarginal striae in early ontogeny; (9) pitted left beak, simple ribs, and internal rib carinae; (10) resilial teeth extended and tending to parallel hinge (see text for further explanation).

being completed. Waller (1991, fig. 8) presented an hypothesis of the relationships of major groups and discussed what little can presently be said about the synapomorphies present at each node in a phylogenetic diagram. The phylogenetic events with which the present study is concerned are at finer levels (Fig. 1). In this figure, pairs of clades that comprise sister groups are shown by a U-shaped branching pattern; paraclades, which cannot yet be characterized on the basis of unique apomorphies, are shown as continuations of stem lineages. The tribe Chlamydini, for example, is a clade that is the sister group of a clade consisting of the tribes Crassadomini (new tribe), Mimachlamydini (new tribe), and Aequipectinini. The tribes Crassadomini and Mimachlamydini are each paraclades in the light of present knowledge. The tribe Crassadomini is the continuation of the stem group for the tribes Mimachlamydini and Aequipectinini; the tribe Mimachlamydini is a continuation of the stem group for the tribe Aequipectinini, the latter being a true clade in that its members share unique derived features.

The family Pectinidae (Node 2 in Fig. 1) is rooted in a single but universal apomorphy, a ctenolium along the ventral edge of the byssal notch of the right valve (Waller, 1984). The subfamily Camptonectinae is viewed as the paraphyletic stem group from which all other Pectinidae were derived and is at present characterized by plesiomorphic features. Specifically, the subfamily is sculpturally simple, without strong radial ribbing, microsculpture dominated by a simple pattern of broadly sweeping antimarginal striae (*"Camptonectes striae"*), and an anterodorsal disk margin that is concave in lateral view. (See Waller (1991) for a more detailed discussion.)

The subfamilies Chlamydinae and Pectininae are joined at Node 3 (Fig. 1) by the advent of coarse ribbing and the straightening of the anterodorsal disk margin. As discussed by Waller (1991), these subfamilies (each referred to in that paper as a series of groups) were already in place well before the end of the Mesozoic era, where they are respectively exemplified by the genera *Lyriochlamys* Sobetski, 1977, and *Microchlamys* Sobetski, 1977. Although the subfamily names Chlamydinae and Pectininae used in the present study are based on the generic names *Chlamys* and *Pecten*, each associated with a well-known shell shape, these shapes are in no way characteristic of an entire subfamily. The chlamydoid form is probably plesiomorphic, but the pectinoid form (as in *Pecten, sensu stricto*) and other forms such as those associated with the genera *Amusium* and *Aequipecten* have evolved repeatedly and independently in both subfamilies. At present these subfamilies are based mainly on extensive linkages between extinct lineages (Waller, unpub. data) and are difficult to define or diagnose on the basis of universal synapomorphies. In general, however, there is an approximate difference in the style of hinge development, with the Chlamydinae (Node 5) emphasizing resilial teeth and the Pectininae (Node 4) emphasizing dorsal and intermediate teeth (Waller, 1991, fig. 6). Also in an approximate way, the Chlamydinae display greater microsculptural complexity than do the Pectininae.

Enumeration of apomorphies within the Chlamydinae (i.e. above Node 5, Fig. 1) becomes more straightforward and is taken up in the following discussion of tribes present in the Caribbean and adjacent regions.

Subfamily Chlamydinae von Teppner, 1922

Discussion.— Based on comparison with taxa in Mesozoic outgroups such as the Camptonectinae and *Lyriochlamys* in the Chlamydinae, it seems likely that primitive characters in the Chlamydinae include commarginal lirae in interspaces, a small posterior auricle with a concave posterior margin, and microsculpture consisting of antimarginal striae arrayed in a broad sweeping *"Camptonectes"* pattern that is continuous across radial ribbing. This pattern of antimarginal striae begins early in ontogeny at the edge of the prodissoconch on the left valve and at the edge of the prismatic stage on the right valve. The primitive radial ribbing pattern is complex in the sense that rib introduction by both branching and intercalation is present in the same individual and commonly on the same valve. The ribs themselves, however, are simple corrugations, without carinate edges on the shell interior (Waller, 1991, fig. 5).

An important change occurred in shell microstructure between Cretaceous *Lyriochlamys* and the modern Chlamydinae beginning in the late Cretaceous and early Paleocene (Waller, 1991; Waller and Marincovich, 1992; Fig. 1, Node 6). This involved the withdrawal of the area of deposition of crossed lamellar aragonite on the shell interior to a position bounded distally approximately by the pallial line, in contrast to Cretaceous and earlier *Lyriochlamys,* in which aragonite deposition extended nearly to the shell margins and comprised most or all of the hinge structures.

The subfamily Chlamydinae can be subdivided into four extant tribes related as shown in figure 1. The apomorphies for each branching point are as follows:

Node 7 (Chlamydini). The character that forms the basis for the tribe Chlamydini is shagreen microsculpture, a screenlike pattern formed by the offset contacts of frilled commarginal lamellae (Fig. 2; see also Waller, 1972, 1991, and Hayami and Okamoto, 1986). Although this structure is not universally present in all extant members of this tribe, the succession of morphologies among extant and fossil species suggests that it was present initially in the basal lineages contained in the clade. In contrast, no

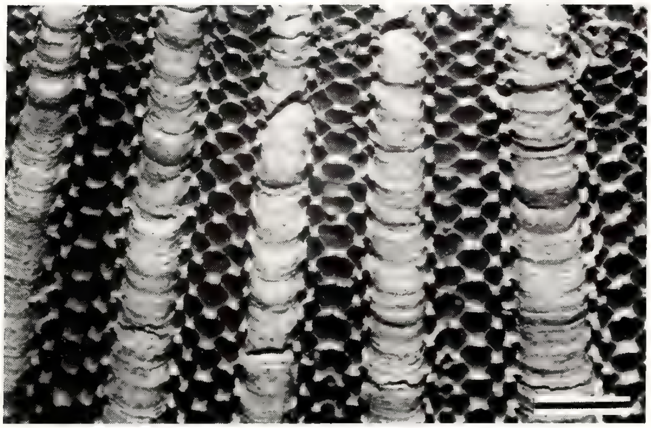

Fig. 2. Shagreen microsculpture in center of left valve of *Chlamys islandica,* USNM 764635, Recent, off Godhaven, Greenland (ht. of valve = 20 mm, scale bar = 1.0 mm).

unequivocal shagreen microsculpture is known among extant or fossil members of the tribes Crassadomini (new tribe), Mimachlamydini (new tribe), and Aequipectinini, which collectively comprise the sister group of the Chlamydini. Where commarginal lirae are present in the Chlamydini, they begin after the start of radial ribbing. This allows the plesiomorphic sweeping pattern of antimarginal striae to be prominent in very early ontogeny, before the beginning of the radial stage on the left valve and continuing at least through the early part of that stage. The more derived lineages in the Chlamydini, which will be discussed in greater detail below (under *Laevichlamys,* new genus), lose both commarginal lirae and shagreen microsculpture altogether and develop numerous intercalated costae in the interspaces of major ribs, tending to fill the interspaces completely (Fig. 4). As will be shown below, true *Hinnites* and the genus *Pedum* Lamarck, 1799, are both within this tribe. The subfamily names Hinnitinae Habe, 1977, and Peduminae Habe, 1977 (*sic,* emended to Pedinae) are therefore reduced in rank and made junior synonyms of Chlamydini.

Node 8 (Crassadomini + Mimachlamydini + Aequipectinini). The only synapomorphy that unites these groups is the loss of the plesiomorphic sweeping pattern of antimarginal striae in the early radial stage. Instead, commarginal lirae tend to dominate microsculpture at least between the proximal ends of the simple radial ribs (Figs. 5, 7). The microsculpture of the left-valve pre-radial region in the Crassadomini is variable, ranging from interrupted antimarginal striae (Fig. 7g) to a pitted or nearly smooth condition (Fig. 5d). There is a trend toward simplification of ribbing patterns. Medial intercalations, present on both valves in many Chlamydini and in Mesozoic *Lyriochlamys,* become rare on right valves except for a few examples of secondary origin of precisely medial intercalary costae (e.g. in *Spathochlamys,* new genus, described below).

The plesiomorphic state of ribbing cross-sections at Node 8 (Fig. 1) remains as simple corrugations, without internal carinae on mature shells. The hinge also remains in its plesiomorphic state as in the Chlamydini, consisting of a simple two-element structure, with the dorsal teeth and resilial teeth being of about equal strength in most taxa.

Node 9 (Mimachlamydini + Aequipectinini). Three apomorphies unite the tribes Mimachlamydini and Aequipectinini: (1) Left-valve beaks display a densely pitted microsculpture (Waller, 1991, figs. 4b, 9c,d), although as previously stated this feature was already making its appearance in some Crassadomini; (2) the ribbing pattern becomes further simplified, with the ribs that are introduced in early ontogeny commonly being the only ribs or at least remaining as the major ribs throughout ontogeny (Figs. 10, 11); (3) the edges of the ribs on inner surface of the shell become carinate (Figs. 10h, m). These carinae are variably expressed in populations of extant *Mimachlamys varia* but consistently developed in many other extant and extinct members of this clade. The hinge of the Mimachlamydini retains its basic plesiomorphic two-element structure, as in the Chlamydini and Crassadomini, although some extinct *Mimachlamys* show some thickening and incipient bifidity of the resilial teeth of the right valve. Shell shape remains *Chlamys*-like in the Mimachlamydini, as does the shape of

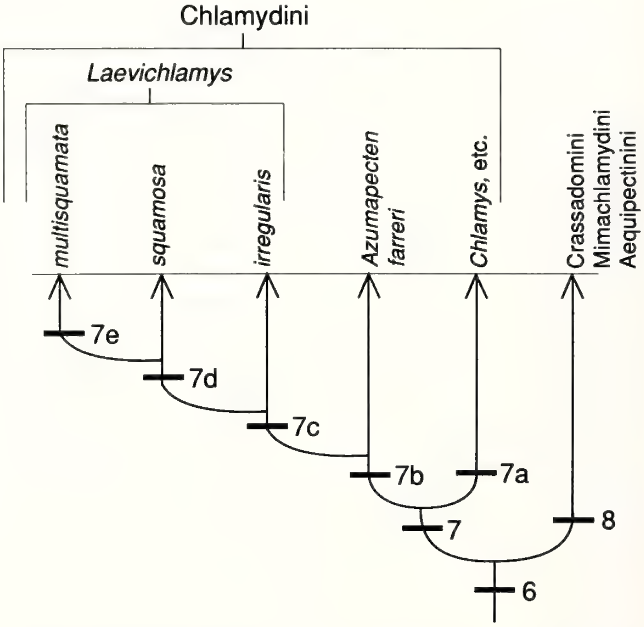

Fig. 3. A phylogeny showing derivation of the new genus *Laevichlamys* within the tribe Chlamydini (numbered blocks refer to apomorphies; those numbered 6, 7, and 8 are as shown in figure 1; see text for explanation).

the posterior auricle, which generally retains a concave posterior margin.

At Node 10 (Fig. 1), the tribe Aequipectinini is marked by the onset of a hinge structure dominated by resilial teeth, which enlarge and extend anteriorly and posteriorly, nearly paralleling the dorsal teeth (Waller, 1991, pl. 5, fig. 14). There are attendant changes in valve symmetry, shape becoming more equilateral and the anterior and posterior auricles more equal in size. Lastly, there is a sculptural change in the early commarginal lirae, which display a ventrally concave looped trend on the rib flanks, at least in the early ontogeny of many taxa.

This basic framework of four extant tribes in the Chlamydinae was already in place by the Eocene epoch, 36 million years ago (Waller, 1991). The main evolutionary radiation of these tribes, however, did not become extensive until the beginning of the Miocene, when the proto-Mediterranean was still open at its eastern end to the Indian Ocean and the Caribbean was still open to the eastern Pacific. The search for ancestors of extant Caribbean species in these tribes therefore should not be limited to the western Atlantic and eastern Pacific.

Tribe Chlamydini von Teppner, 1922

Diagnosis.— Chlamydinae retaining in early ontogeny a microsculptural pattern of continous antimarginal striae that sweep across early radial ribbing; shagreen microsculpture present at least in early lineages.

Discussion.— Six extant species in the Caribbean and adjacent western Atlantic waters have traditionally been placed in the genus *Chlamys, sensu stricto,* because of their asymmetric auricles (the anterior one the longer) and deep byssal notch floored by an ontogenetically persistent ctenolium: *Chlamys benedicti* Verrill and Bush, 1897, *C. imbricata* (Gmelin, 1791), *C. mildredae* (Bayer, 1941), *C. multisquamata* (Dunker, 1886), *C. ornata* (Lamarck, 1819), and *C. sentis* (Reeve, 1853). In the present study, these species are found to represent three tribes in the Chlamydinae (Table 1), and none can be assigned to *Chlamys* unless that name is used so broadly as to encompass almost the entire subfamily.

The sole extant member of the tribe Chlamydini in the tropical and subtropical western Atlantic is *"Chlamys" multisquamata.* This species, with its flattened form, flaring disk, and fine sculpture (Figs. 4a-i, l, m), stands apart from the other Caribbean species and is strikingly similar to *"Chlamys" squamosa* (Gmelin, 1791) of the western Indo-Pacific (Figs. 4j, k, n). The resemblance extends beyond the flattened streamlined form of these species. There are also strong similarities in ribbing pattern, early microsculpture, color pattern, and the strong dorsal projection of the dorsal margin of the right anterior auricle. Resemblance even extends to the common presence of a tiny dense pattern of curved intersecting white pigment lines that appears on the beaks before the end of the prismatic stage of the right valve. This same pigmentation pattern occurs in several Indo-West Pacific chlamydoid species but is especially common in *"Chlamys" squamosa* and its close relatives. To appreciate whether these similarities are shared derived characters, and, if so, how a western Atlantic species can be related to a western Indo-Pacific species with no apparent intermediate geographic links in either the eastern Pacific or the eastern Atlantic, requires an overview of the tribe Chlamydini as here defined.

Figure 3 diagrams a phylogenetic pathway through an array of species in the tribe Chlamydini that show important differences in microsculpture and ribbing patterns. It is important at this point to review the plesiomorphic conditions that were present (Node 6) before the origin of the Chlamydini, because these conditions help to polarize the derived states that provide crucial phylogenetic information. The plesiomorphic character states at Node 6 are as follows:

1) Shell shape acline or prosocline, not markedly opisthocline or opisthogyrate, with a deep byssal notch.

2) Dorsal auricular margins not sharply folded and not projecting dorsally very far beyond the outer ligaments.

3) Ontogenetic transgression of an inner layer of foliated calcite ventrally from the dorsal region across the umbonal region absent; aragonite (most commonly crossed-lamellar except in muscle attachment scars) present throughout the region inside the pallial line.

4) Posterior auricles small but with their posterior margins concave in shape, with the overall trend of the margin forming nearly a right angle with the hinge line.

5) Antimarginal striae in a broad sweeping pattern with trends not significantly interrupted by radial ribbing, at least in the early ontogeny of the radial stage.

6) Left-valve beak sculpture exhibiting the same antimarginal pattern as in the early radial stage; beak secondarily smooth in some taxa, but seldom coarsely pitted.

7) Commarginal lirae present in interspaces during at least part of ontogeny.

8) Several modes of rib introduction present on same shell, including branching, rib-flank intercalation, sub-medial intercalation, and medial intercalation on a single valve.

9) Ribs in the form of simple radial folds, without

thickening of edges on the shell interior, i.e., without internal rib carinae.

The base of the Chlamydini (Node 7, Figs. 1, 3) is marked by the advent of shagreen microsculpture (Fig. 2). The primitive expression of this is probably as small patches in rib interspaces on the disk and auricles. Extensive shagreen over virtually the entire shell seems to be a derived condition that has been reached independently in different species lineages, most notably in the *Semipallium* group (see Waller, 1991, fig. 10).

The lineage marked *"Chlamys,* etc." on Figure 3, Node 7a, marks a polytomous assemblage of groups some of which appeared early in the radiation of the tribe. Among these are genera such as *Chlamys, Zygochlamys, Talochlamys, Semipallium,* and even the *Patinopecten* group, each characterized by a set of autapomorphies. *Chlamys, sensu stricto,* contains species exemplified by (1) the type species of the genus, *Chlamys islandica* (Müller, 1776), living in the northeastern and northwestern Atlantic, (2) a group of closely related northern Pacific species including *C. albida* (Arnold, 1906, [ex Dall MS]), *C. behringiana* (Middendorf, 1849), *C. rubida* (Hinds, 1845), and *C. hastata* (Sowerby, 1842), and (3) the eastern Atlantic cemented species *"Hinnites" ercolanianus* (Cocconi, 1873). These taxa are all united by a byssal notch that is shallower than the plesiomorphic state, by a foliated-calcite transgression, and by an early irregularity in the antimarginal microsculpture before the advent of the first shagreen microsculpture. The expression of shagreen microsculpture is highly variable among and within species of *Chlamys, s.s.,* and even within population samples. In the eastern Pacific, for example, there is some evidence of a southward disappearance of shagreen microsculpture in the sequence *C. albida, C. hastata hastata, C. hastata hericea,* a sequence that also displays increasingly derived macrosculptural patterns.

Chlamys, as here restricted, appears to have originated in the Pacific and entered the eastern Pacific and northern Atlantic via northern routes (Waller, 1991). *Chlamys islandica* itself penetrated as far south as the Mediterranean during cold pulses of the Pleistocene (Roger, 1939: p. 170). *"Hinnites" ercolanianus* (Cocconi, 1873), of which *Hinnites absconditus* P. Fischer in Locard, 1883, is a junior synonym (Adam, 1960), presently lives in the eastern South Atlantic off the Cape Verde Islands and along the Atlantic coast of Africa from the Gulf of Guinea (4° 44'N) to northern Angola (8° 30'S) at depths in the 100 to 200 m range (Adam, 1960; Waller, unpub. data). The living members of this species, however, are but a relict of a much more widespread occurrence in the Pliocene of the Mediterranean (Raffi, 1971) and the Miocene of Belgium (Glibert, 1945, referring to the Anversian or Serravalian stages). The ancestor of this species, which is considered to be *"H." brussoni* (de Serres, 1829) from the Burdigalian of southern France (Roger, 1939: p. 175), has shagreen microsculpture.

In spite of the long history of *Chlamys, s. s.,* no member of this genus is known to be living in the present-day tropical American regions that are the subject of the present study. As will be shown below, taxa from these regions that have been referred to *Chlamys* in fact belong to other genera with very different histories.

Three derived features are important at Node 7b (Fig. 3): (1) the advent of a somewhat opisthocline and opisthogyrate shell form; (2) a straightening (loss of concavity) of the posterior margins of the posterior auricles, these margins becoming straight or even convex; and (3) an increase in the frequency of rib introduction by intercalation. Shagreen microsculpture is retained at this node, as is also the plesiomorphic absence of a foliated calcite transgression on the shell interior. This stage of phylogenetic development is characterized by the genus *Azumapecten* Habe, 1977, of which *A. farreri* (Jones and Preston, 1904) is the type species. The shell shape and deep byssal notch suggest that this level represents an increased adaptation to byssate life, a conclusion that is corroborated by increasingly common shell irregularity in response to growth in confined spaces. Geographically, this stage of development among extant species seems to be limited to the western Indo-Pacific.

At Node 7c (Fig. 3), the following derived features appear: (1) increase in rib introduction by intercalation to the point that rib interspaces are eliminated in late ontogeny; (2) the ontogenetically late appearance of the first radial ribs, allowing a zone of prominent coarse antimarginal striae to develop in the pre-radial stage of the left valve; (3) disappearance of shagreen microsculpture from at least the center of the disk and usually from the entire shell; (4) trend of posterior margins of posterior auricles forming an oblique angle with the hinge line, the margins themselves being most commonly nearly straight or only slightly concave or convex. Also at this stage is a common presence of a minute net of white pigment lines in very early ontogeny, still within the prismatic stage of the right valve. This stage and the following one characterized by rib crowding and the ontogenetic disappearance of interspaces encompass species placed in *Laevichlamys,* new genus. The stage at Node 7c is best represented by species such as *L. irregularis* (G.B. Sowerby II, 1842) and *L. wilhelminae* (Bavay, 1904) (see illustrations in Waller, 1972b, where these species were referred to as *Chlamys irregularis* and *C. marshallensis* Waller, 1972, the latter name being a junior synonym of Bavay's name).

Node 7d (Fig. 3) is marked by (1) decreased shell convexity, (2) dorsal projection of the dorsal margins of the right-valve auricles, particularly that of the right anterior auricle, and (3) marked obliquity and common convexity of the posterior auricular margins. This stage is exemplified by *Laevichlamys squamosa* (Figs. 4j, k, n).

Finally, Node 7e is marked by the advent of sharp recurvature of the right anterior auricle's dorsal margin and a recurvature of the dorsal margin of the right posterior auricle to produce a slight trough along this margin (Fig. 4c, arrow). The convex curvature of the posterior margin of the posterior auricles and the trend of this margin to produce a very oblique angle with the hinge (Fig. 4g) are both more extreme than in *L. squamosa* (Fig. 4k). These features represent the most derived states of characters already present at Node 7b, and this stage is represented by a single extant species, *L. multisquamata* of the western Atlantic.

The morphological trends from *Azumapecten* to advanced *Laevichlamys* are not exclusively exemplified by these genera, because there are other generic names that have been introduced on the basis of "degree of difference" considerations. The monotypic Indo-west Pacific genus *Pedum* Lamarck, 1799, for example, exhibits a bizarre shell form because it lives embedded and entrapped in massive hard corals such as *Porites* (Yonge, 1967; Waller, 1972; Kleemann, 1990). The early growth stage of this taxon, however, has closely packed intercalated ribs, a projecting right anterior dorsal margin, and oblique posterior auricles that suggest derivation from above Node 7d (Fig. 3), probably from *Laevichlamys squamosa* or a similar species. *Coralichlamys* Iredale, 1939, a less bizarre, irregularly shaped, secondarily commarginally lamellate genus that lives embedded in coral in the Indo-Pacific, may also be monotypic. Its morphology suggests derivation from above Node 7b (Fig. 3). The Indo-Pacific genus *Scaeochlamys* Iredale, 1929, represented by two extant species, *S. livida* (Lamarck, 1819) and *S. tegula* (Wood, 1828), is characterized by a strongly opisthogyrate form, flattened right valve, and hypertrophied scales on major ribs. Its auricular shapes and presence of shagreen both indicate that it is above Node 7b.

Based on the geographic distribution of living and fossil species, the early evolutionary radiation of the Chlamydini above Node 7b (Fig. 3) was apparently mainly within the tropical to warm-temperate western Pacific and Indian oceans, because no primitive *Laevichlamys* are known from the eastern Pacific, the western Atlantic, or the eastern Atlantic. This Indo-Pacific evolutionary radiation of *Laevichlamys* seems to have been well underway by the Late Miocene, but the extent of the radiation by that time is difficult to judge because of the very meager Miocene fossil record on low, reef-dominated tropical Indo-Pacific islands. If the radiation of advanced *Laevichlamys* (Nodes 7c and 7d, Fig. 3) occurred no earlier than Late Miocene, then its dispersal from the Indian Ocean to the Caribbean by way of the proto-Mediterranean would not have been possible, because the eastern portals of the Mediterranean were effectively closed by the end of the early Miocene (late Burdigalian; Adams *et al.,* 1983, 1990; Piccoli *et al.,* 1986; Por, 1989). Alternatively, entry into the Atlantic may have been by way of chance dispersal from the Indian Ocean around the southern tip of Africa. In either case, one would expect some evidence of the presence of advanced *Laevichlamys,* either living or fossil, in the eastern Atlantic.

The search for evidence of dispersal of *Laevichlamys* between the Indian Ocean and the Atlantic has led to one of the most surprising findings of the present study. A probable descendant from *Laevichlamys* turns out to be an extant cemented species of the eastern Atlantic, *Hinnites corallinus* (G.B. Sowerby I, 1827), which in turn may prove to be the same as the presumably extinct type species of the genus *Hinnites, H. crispus* (Brocchi, 1814), known mainly from the Mediterranean Pliocene. The evidence that has led to this interpretation is as follows:

1) Specimens reported by Kensley (1985) from Namibia were determined by me (pers. comm. to Kensley, 1985) to represent two species of *"Hinnites"*. One of these, found in Cape Province, South Africa, is the familiar *"Hinnites" ercolanianus* (Cocconi, 1873), previously known from the Angolan coast (see Adam, 1960). As mentioned above, *"H." ercolanianus* is derived from a shagreen-bearing ancestor and is probably referable to *Chlamys, sensu stricto*. In the same personal communication quoted by Kensley, I suggested that the second species from Namibia is possibly new. It was distinguished from the former on the basis of the macro- and microsculpture of the early *Chlamys* stage. As shown in Figures 4o to 4r, this Namibian *Hinnites* has a pattern of rib introduction like that present in *Laevichlamys*, where rib interspaces are filled by the repeated medial intercalation of new radial costae. Furthermore, a close relationship to *L. squamosa* is indicated by auricular shapes, the dorsal margin of the right anterior auricle extending prominently above the hinge line and the posterior margin of the posterior auricle exhibiting a convex outline tending to form an oblique angle with the hinge. Lastly, some specimens of the Namibian species show the minute net of white pigment lines that is common in species above Node 7b in Figure 3. Although Kensley (1985) thought that the specimens of this Namibian species were fossil, the immature shells show little sign of wear and have adhering ligamental material.

2) Cosel and Gofas (1984), in a paper that I received after the aforementioned identification for Kensley (1985) was completed, described a new cemented pectinid species, *Hinnites spectabilis* Cosel and Gofas, 1984, which

they reported as living along the southern part of the coast of Angola. Their description and illustrations leave no doubt that this is the same as the Namibian species.

3) Cosel (pers. comm., August, 1992) examined the type specimen of *Hinnites corallinus* G.B. Sowerby I, 1827, originally said to come from East Africa, and determined that it is the same as the species that he and Gofas (1984) had described as new. The East African locality is apparently in error.

4) The macro- and microsculpture of the *Chlamys* stage of *Hinnites corallinus* is remarkably similar to that of the type species of *Hinnites*. The latter is *H. crispus* (Brocchi, 1814), a fossil originally described from the Pliocene of Italy. The fossil species tends to be larger in size and thicker shelled than the living one, but there are broad similarities in form as well as in sculptural detail (see Roger, 1939). It is possible that these differences are ecophenotypic and that these species may be synonymous, in which case the living east African specimens are but a relic of a previously more broadly distributed species.

5) If it is true that *Hinnites crispus* is derived from an ancestral species in the new genus *Laevichlamys,* then the fossil record of *H. crispus* tends to support the idea that *Laevichlamys* did not enter the Atlantic by westward dispersal across the proto-Mediterranean. This is because the oldest specimens of *H. crispus* are known not from the Mediterranean but from the Atlantic side of France (Helvetian of the Aquitaine Basin and Loire Valley; Roger, 1939). Although the species has been reported from the late Miocene (Tortonian) of Austria, Hungary, and Bulgaria (Cuenca, 1980: 62; Raffi: 1971:124), it did not become widely distributed in the Mediterranean until the Pliocene, at which time it also extended as far as the British Isles (Roger, 1939: 174). Roger (1939: 174) thought that the species persisted into the late Pleistocene (Sicilian) in the western Mediterranean based on specimens from the Alpes-Maritimes region of France. Unfortunately, there is no Miocene or Pliocene fossil record of *H. crispus* (or *H. corallinus*) in southern Africa, nor is there any fossil record of a preceding free-living *Laevichlamys* in the eastern Atlantic.

6) The fossil record of the Caribbean species, *Laevichlamys multisquamata,* discussed below, is no older than Pleistocene.

A reasonable interpretation of this evidence is that a species of advanced *Laevichlamys* had entered the eastern Atlantic from the Indian Ocean by late Miocene time via a route around southern Africa. A derivative of this species adopted a cemented mode of life, evolved into true *Hinnites,* dispersed into the Mediterranean through its western portal after the end of the Miocene, and nearly became extinct during the late Pliocene and early Pleistocene climatic cooling that profoundly affected the early Pliocene fauna of the Mediterranean (Raffi *et al.*, 1985). If the extant *Hinnites corallinus* is indeed synonymous with *H. crispus,* then the species survives today in refugia along the west African coast. It seems likely that another propagule of *Laevichlamys* dispersed to the tropical Western Atlantic and evolved, during the Pleistocene, into *Laevichlamys multisquamata.* This species has no geminate sister species in the eastern Pacific because it originated in the tropical western Atlantic region after the closure of connecting seaways.

Laevichlamys, new genus

Etymology.— The name *Laevichlamys* is derived from the Latin word *levis* (or *laevis*), meaning smooth, with reference to macrosculpture of low relief, and the genus name *Chlamys.*

Diagnosis.— Non-cemented Chlamydini with shagreen microsculpture secondarily absent at least on central sector of disk and commonly on entire shell; radial ribs initially low, tending to originate in ontogeny well after end of prismatic stage, and preceded by zone of uninterrupted antimarginal striae; rib introduction mainly by repeated intercalation medially in interspaces of preceding ribs on both valves, nearly or entirely filling interspaces between ribs; regular commarginal lirae absent.

Type species.— *Pecten multisquamatus* Dunker, 1864, living, tropical western Atlantic.

Other species.— In addition to the type species, extant species included in the new genus are as follows: *Pecten irregularis* G.B. Sowerby II, 1842; *P. lemniscatus* Reeve, 1853; *P. limatulus* Reeve, 1853; *P. mollitus* Reeve, 1853; *P. ruschenbergeri* Tryon, 1869; *Ostrea squamosa* Gmelin, 1791; and *Chlamys wilhelminae* Bavay, 1904. All of these live in the Indo-Pacific region.

There is still much to learn about the fossil record of this genus, but two extinct species are included thus far: *Pecten (Chlamys) lauensis* Ladd in Ladd and Hoffmeister, 1945, Fiji, late Miocene or Pliocene; *P. shirahamaensis* Nomura and Niino, 1932, Japan, Early Pliocene (Masuda, 1962, p. 185).

Geographic range.— Western Indo-Pacific and western Atlantic.

Stratigraphic range.— Upper Miocene to present.

Discussion.— As argued in the preceding section dealing with the tribe Chlamydini, the new genus *Laevichlamys* probably has a tropical Indo-Pacific origin, and morphologically advanced species entered the eastern Atlantic in the late Miocene probably via a southern African route of dispersal. The former presence of the genus in the Mediterranean and eastern Atlantic is indicated by the presence in these areas of *Hinnites,* which likely evolved from a species of *Laevichlamys.*

Laevichlamys is paraphyletic in that specialized, derived genera such as *Hinnites* DeFrance, 1821, and *Pedum* Lamarck, 1799, are excluded (see preceding discussion of the tribe Chlamydini). The alternative to achieve a holophyletic status would be to broaden the concept of the genus to include all of these, but the name based on priority would then become *Pedum,* a taxon well-known for its highly unusual form and specialized living habit embedded in massive corals. This would clearly raise havoc with the morphological concepts that have long been attached to particular names.

Laevichlamys multisquamata (Dunker, 1864)

(Figures 4a-i, l, m)

Pecten multisquamatus Dunker, 1864: 100, Recent, Havana Bay, Cuba.

Pecten multisquamatus Dunker, 1864. Dunker, 1865: 67, pl. 23, figs. 1-3.

Pecten effluens Dall, 1886: 219, Recent, off Havana, 127 fathoms [232 m].

Chlamys effluens (Dall, 1886). Verrill, 1897: 59.

Chlamys multisquamata (Dunker, 1864). Waller, 1973: 41, figs. 9-11.

Types.— The specimen illustrated by Dunker (1865), a pair of matching valves, is of the same dimensions given in his original description in 1864 and would be the logical choice for a lectotype. It is not known, however, whether this specimen still exists. I did not find it among Dunker's material in the collections of the Humboldt University Museum of Berlin, raising the possibility that it may still be in Cuba, perhaps in the collection of J. Gundlach, from whom Dunker received his specimens. According to Dr. José Espinosa of the Instituto de Oceanologìa of Cuba (pers. comm., 1993), however, no specimens of *Pecten multisquamatus* are present in that collection. A second, smaller pair of matching valves from Cuba that bears one of Dunker's manuscript names is housed with some of Dunker's collection in the Humboldt University Museum in Berlin. This specimen, a pair of matching valves collected by Felipe Poey from Cuba, is selected herein as the lectotype of *P. multisquamatus.* Its dimensions are height, 43.1 mm, length 39.5 mm, convexity of articulated valves 8.0 mm, length of anterior outer ligament 10.8 mm, and length of posterior outer ligament 5.0 mm.

Dall (1886) provided no illustration with his original description of *Pecten effluens* but referred to the largest valve as having a height of 26.0 mm and a width of 22.0 mm. In the type collection of the National Museum of Natural History, the lot marked "types" (USNM 62236) contains a left valve and a smaller, non-matching right valve. The left valve, although conforming to Dall's description, is only half the size that he stated. Three years later Dall (1889, pl. 42, fig. 9) illustrated a *Pecten effluens* which he said had a height of 26 mm. This specimen, a left valve, corresponds exactly in shape and ribbing pattern to the left valve in USNM 62236 that is only half the size. It is assumed that Dall misstated the measurements from an enlarged drawing provided by an artist, and the left valve (ht. = 13.2 mm) in USNM 62236 is herein selected as the lectotype of *P. effluens* (Fig. 4h).

Type locality.— Havana Bay, Cuba.

Diagnosis.— *Laevichlamys* of low convexity and streamlined, flaring form, the umbonal angle exceeding 90° for specimens greater than 20 mm in height; dorsal margin of right anterior auricle sharply folded and dorsal margin of right posterior auricle with slight trough; posterior margins of posterior auricles convex, producing distinctly oblique angle with hinge; ribbing retaining low relief throughout ontogeny, with all ribs and riblets having low, tiny, closely spaced scales.

Morphological variation.— *Laevichlamys multisquamata* attains a moderate size, the largest specimens having a shell height of about 70 mm. The amplitude of the first-order radial plicae can vary considerably (compare Figs. 4b and 4f). The surfaces of some specimens are nearly flat, with only the fine costae present or with the first-order radial plicae limited to early ontogeny. The yellowish tinge on the umbones illustrated by Dunker (1865) and referred to by Dall (1886) is common but not present on all specimens.

Comparison.— The morphology of *Laevichlamys multisquamata* is unique among chlamydoid scallops in the western Atlantic and eastern Pacific. The early, *Chlamys* stage of *Hinnites corallinus* of the eastern Atlantic off west Africa (see preceding discussion of the tribe Chlamydini) is similar but differs in having more prominent and persistent first-order radial plicae and in having less numerous secondary intercalated radials. Among Indo-Pacific *Laevichlamys,* the species that is closest in morphology is *L. squamosa* (Waller, 1972, pl. 3, figs. 38-41, and Figs. 4j, k, n herein). The latter differs from *L. multisquamata* in

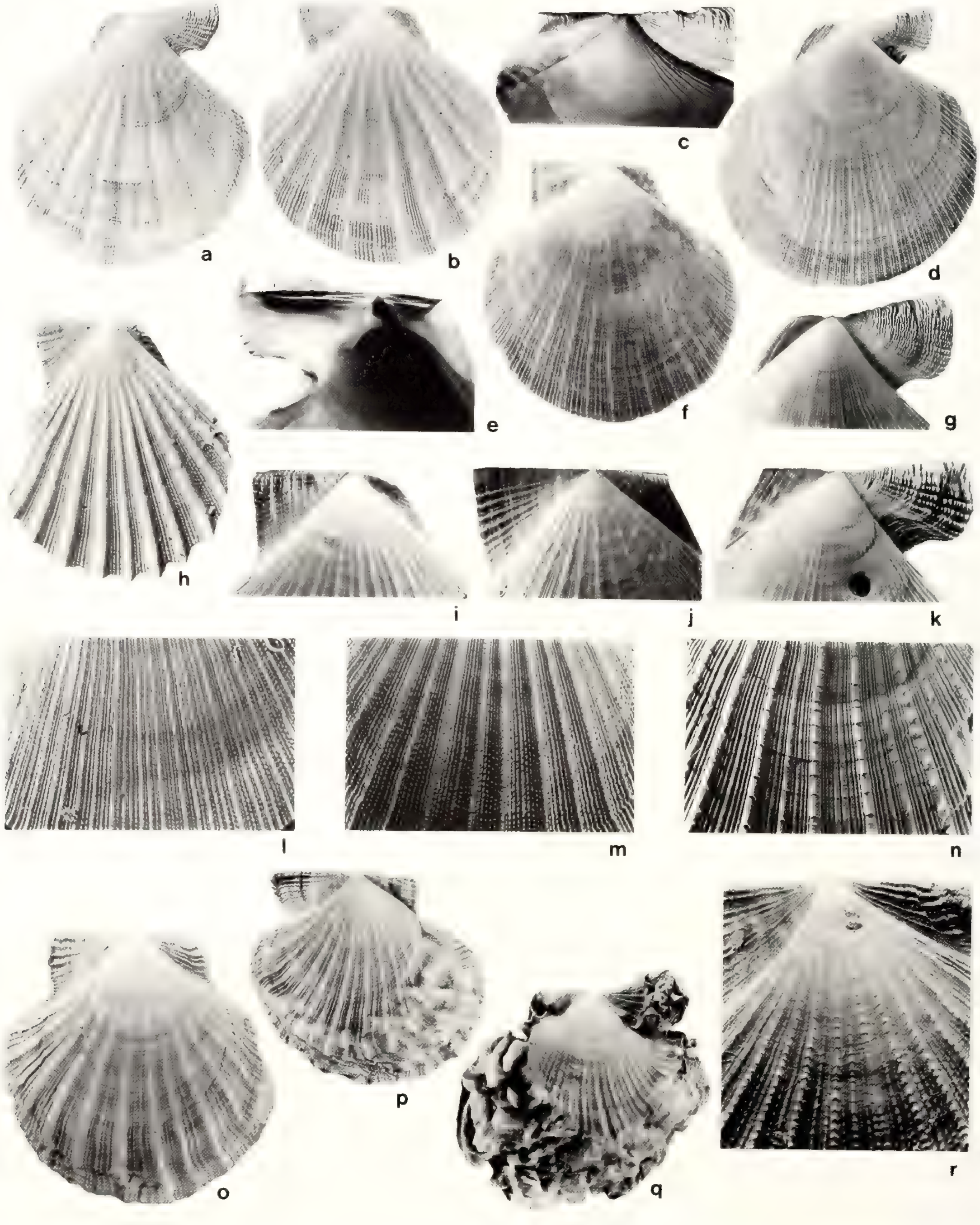

Fig. 4. *Laevichlamys* (a-m) and *Hinnites* (n-q). **a, b**. *L. multisquamata,* USNM 764750, Guadeloupe, West Indies, matching right and left valves, height 26.1 mm. **c, e.** *L. multisquamata,* USNM 846201, off Boynton Beach, Florida, dorsolateral view of right dorsal margin showing trough (arrow) on posterior auricle and interior view of right hinge, hinge length 7.2 mm. **d, f.** *L. multisquamata,* USNM 710926, south coast at St. Luce, Martinique, West Indies, matching right and left valves, height 47.9 mm. **g, i, l.** *L. multisquamata,* USNM 764749, La Chorerra, Havana, Cuba, right dorsal exterior, hinge length 23.2 mm., non-matching left dorsal exterior, hinge length 14.2 mm., and details of sculpture on same right and left valves, horizontal field widths both 26 mm. **h**. *L. multisquamata*, USNM 62236, probably Dall's illustrated specimen of *Pecten effluens*, off Havana, Cuba, left valve, height 13.3 mm. **j, k, n.** *L. squamosa*, USNM 846209, Manaua Id., Fiji, dorsal exteriors of matching left and right valves, hinge length 20.3 mm., and detail of sculpture on left valve, horizontal field width 25 mm. **o-r.** *H. corallinus*, USNM 782400, Bosluisbaai, Namibia, left valve exterior, height 24.4 mm; another left valve, height 38.0 mm; right valve matching preceding; and detail of exterior of preceding left valve, horizontal field width 12.5 mm.

having a narrower umbonal angle (less than 90°) and hence a less flaring aspect, a tendency for scales to be present only on the higher order radial ribs, and in having a less sharply refolded dorsal margin on the right anterior auricle.

Living habits.— *Laevichlamys multisquamata* lives on tropical or subtropical coral reef fronts, between coral or dead shells or in crevices, at depths generally greater than 30 m to well over 100 m; dead shells have been dredged from depths greater than 200 m (Waller, 1973: 47; Abbott, 1974: 443; Sutty, 1986: 102).

Geographic range.— Throughout the Antilles from Barbados northward to southeastern Florida, the Bahamas, and Bermuda (Waller, 1973: 47) and southward to Brazil. The Brazilian record, not previously reported, is based on a right valve found by me in the Paris Museum Collection, where it had been incorrectly identified as *Chlamys ornata*. It is from Calypso Station 45, 11° 22.5'S, 37° 10' W, from a depth of 31 m. A second specimen from Brazil, but without locality details, is present in the BMNH collection. A label indicates that it had been identified by Bavay as *"squamosus* var." In the southern Caribbean, the species extends westward to Panamá (based on a living specimen dredged by the R/V Pilsbry of the University of Miami at a depth of 51 m at 9° 24.8'N, 78° 12.7'W (R/V *John Elliott Pillsbury* Sta. P-417). The species is thus far known from the Gulf of Mexico only from the deep Flower Garden Reef off the Texas coast (Boone, 1978).

Stratigraphic range.— Lower Pleistocene to Recent.

Laevichlamys multisquamata has not previously been reported from the fossil record. In the present study, specimens of this species were found in unidentified collections from the Pleistocene reef deposits of Barbados (BMNH), from undated beds in northern Cuba that are probably no older than Pleistocene in age (PRI), and from the Moín Formation of Costa Rica (USNM). Also, D. G. Robinson (pers. comm., August, 1992) reported finding this species in the topmost beds of the Moín Formation of Costa Rica between plates of the coral, *Agaricia* Lamarck, 1801. The Moín Formation, considered in the past to be early to middle Pleistocene in age (Akers, 1972: 44; Robinson, 1990, 1992), has more recently been considered to include upper Pliocene sediments, although the uppermost part of the formation is still dated as early Pleistocene (Coates *et al.* 1992).

Discussion.— As outlined in the previous discussion of evolution within the tribe Chlamydini, it seems very likely that the ancestor of *Laevichlamys multisquamata* was a species present in the eastern Atlantic during the Late Miocene and Pliocene. Although *L. multisquamata* at present has a broad distribution in the Caribbean region and has been collected from the Caribbean coast of Panamá, no geminate or sister species are known from the eastern Pacific. This would suggest that the origin or at least the dispersal of the species to the western Atlantic has occurred since the closure of seaways by the rise of the Isthmus of Panamá, i.e. since the middle Pliocene. This is corroborated by the negative evidence of the fossil record; thus far no fossils of this species or probable ancestors have been found in rocks that are known to be older than Pleistocene.

Material examined.— Recent material: USNM: 16 lots containing 33 specimens, from southeastern Florida, Bermuda, Cuba, Puerto Rico, the Bahamas, Jamaica, Martinique, Barbados, and Panamá. DMNH: 2 lots containing 2 specimens, from the Bahamas and Jamaica. BMNH: 2 lots containing 2 specimens, from Guadaloupe and Brazil. MNHN: 2 lots containing 6 specimens, from Guadeloupe and Brazil. HUB: 1 lot containing 1 specimen, from Cuba.

Fossil material: BMNH: several specimens, Pleistocene Coral Rock at Bathsheba and Highgate, Barbados. PRI 1257k: a single articulated shell from the D.K. Palmer Collection, Locality 898P: Road cut on Carretera Central, just west of Nena Machado Hospital ["= Bermúdez 5"], Matanzas Province, Cuba. [Locality published in Palmer, 1948.] USNM: USNM(P) 474809, a fragmented left valve, USGS 18693, "colline en démolition," Limón, Costa Rica.

Tribe Crassadomini Waller, new tribe

Diagnosis.— Chlamydinae with shell shape and two-element hinge of *Chlamys,* but without continuous antimarginal striae before beginning of radial ribs; prominent commarginal lirae present in rib interspaces in early ontogeny of left valve or both valves. Left beak microsculpture with discontinuous antimarginal striae, pitted, or secondarily smooth. Rib introductions occurring over much of ontogeny, leading to variously clustered and ordered ribbing patterns; internal rib carinae absent in mature shells, rarely present but weakly developed in juvenile shells.

Discussion.— The pre-radial stage of the left valve in the Crassadomini lacks the plesiomorphic continuously striate condition found in the Chlamydini. In the Crassadomini, commarginal lirae are more prominent than antimarginal striae at the start of the radial stage (Figs. 5, 6), whereas in the Chlamydini, antimarginal striae are more prominent than the commarginals at the same growth stage. No shagreen microsculpture has been detected in any member of the Crassadomini, whereas this feature is present in at least

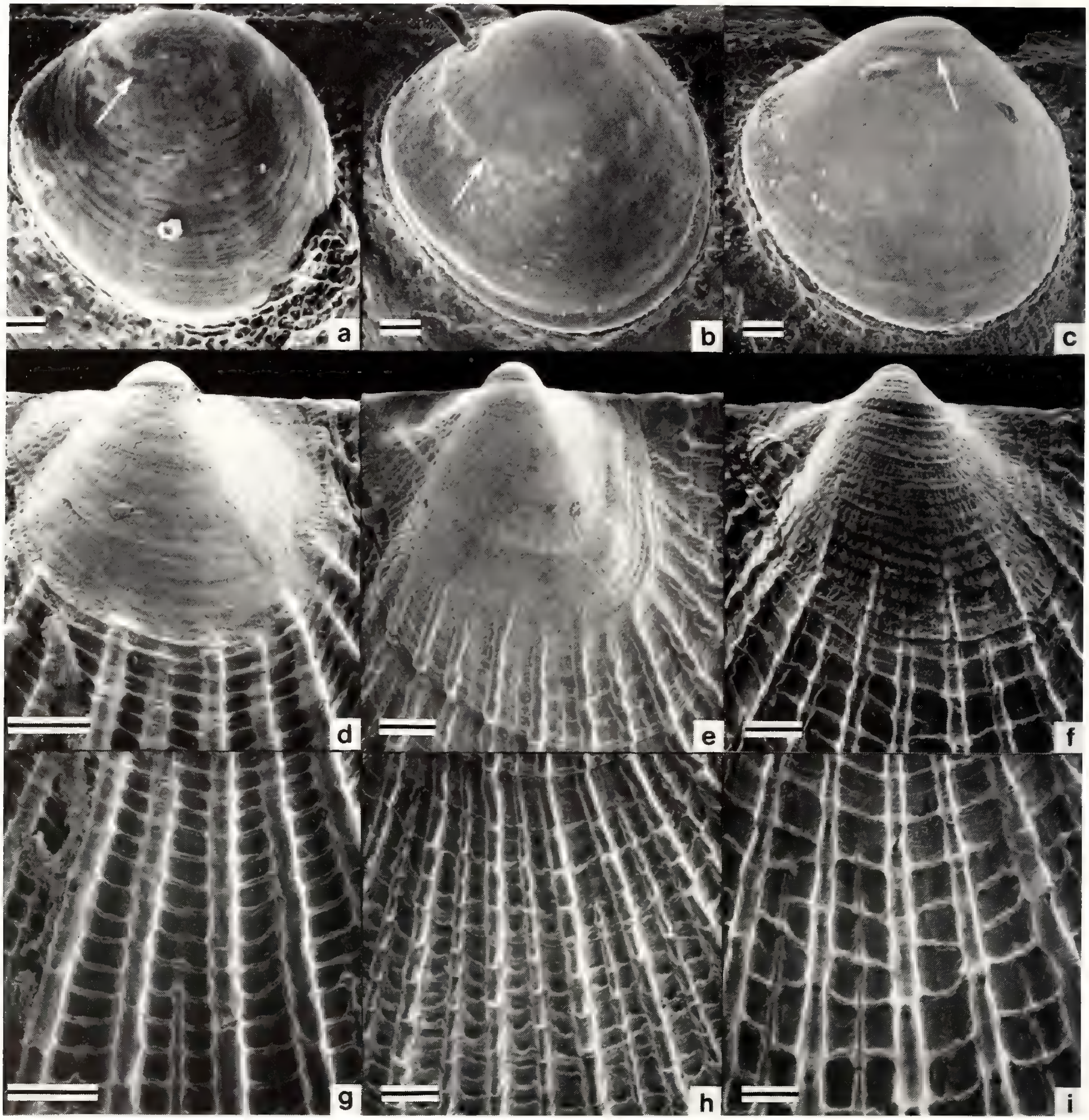

Fig. 5. Scanning electron micrographs of prodissoconchs (a-c), pre-radial stage microsculpture (d-f), and early radial stage sculpture (g-i) of left valves of species of *Crassodoma*. **a, d, g**. *C. multistriata*, USNM 764329, San Pedro Bay, Sao Vicente, Cape Verde Ids. **b, e, h**. *C. pusio*, USNM 196540, Shetland Ids., Scotland. **c, f, i**. USNM 764941, off Long Point, Santa Catalina Id., California. Arrows point to approximate position of PI/PII boundary. Projecting object on anterodorsal side of b is not part of prodissoconch. Scale bars: a-c = 25 µm, d-i = 200 µm.

the early lineages in the Chlamydini.

The style of rib introduction in the Crassadomini is plesiomorphic, with introduction on the right valve being primarily by branching and that on the left valve by intercalation (Figs. 5, 6). This differs from the *Azumapecten-Laevichlamys* clade in the Chlamydini, where intercalation is important on the right valve as well as on the left (Fig. 4). Both the Mimachlamydini and Aequipectinini have simple ribbing patterns in which the primary ribs remain dominant over secondary ribs throughout ontogeny; the edges of these primary ribs have prominent carinae on the inner shell surface (Waller, 1991, fig. 5b; Figs. 10h, m, herein). In contrast, rib introductions in the Crassadomini are spread unevenly during ontogeny to produce variously ordered or clustered rib patterns; these ribs in adults lack internal carinae. Both the Mimachlamydini and Aequipectinini have a

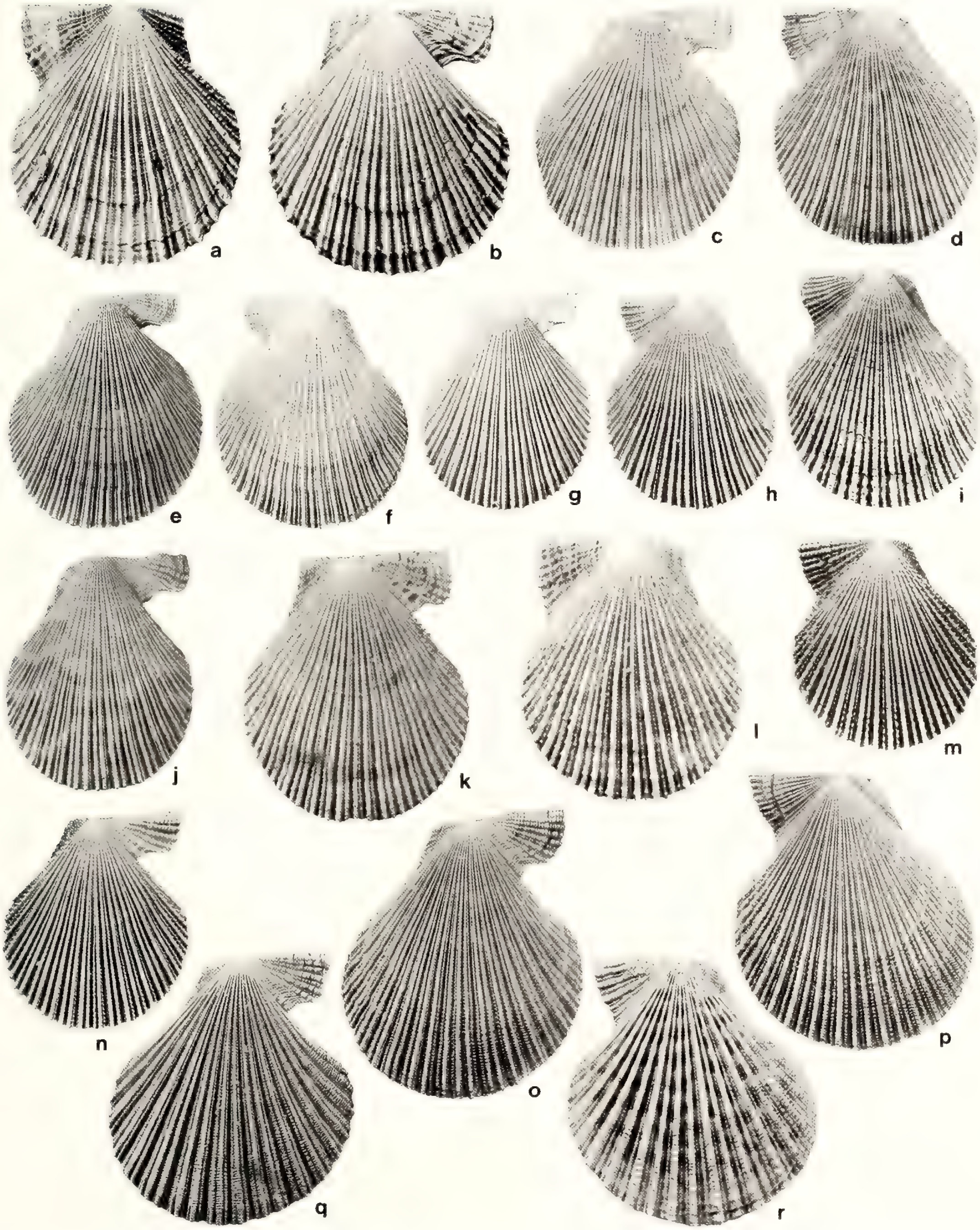

Fig. 6. *Crassadoma* (a-l) and *Caribachlamys* (n-r). **a, b**. *Crassadoma gigantea,* USNM 764946, channel reef, Egmont, British Columbia, Canada, matching left and right valves before cementation, height 16.0 mm. **c, d**. *C. multistriata,* USNM 196495, Naples, Italy, matching right and left valves, height 30.0 mm. **e, f**. Lectotype of *Pecten tinctus* Reeve (= *C. multistriata*), BMNH 1981247/1, locality unknown, matching right and left valves, height 32.5 mm. **g, h**. Lectotype of *P. effulgens* Reeve (= *C. multistriata*), BMNH 1993039/1, locality unknown, matching right and left valves, height 18.8 mm. **i**. Lectotype of *P. textilis* Reeve (= *C. multistriata*), BMNH 1993040/1, locality unknown, single left valve, height 24.9 mm. **j**. paralectotype of *P. textilis* Reeve (= *C. multistriata*), BMNH 1993040/2, locality unknown, single right valve, height 24.4 mm. **k, l**. *C. pusio,* USNM 196511, Langland Bay, Wales, matching right and left valves before cementation, height 13.7 mm. **m, n**. *Caribachlamys sentis,* BMNH 1993041/1, lectotype, locality unknown, matching left and right valves, height 15.9 mm. **o, p**. *C. sentis,* USNM 599341, Venetian Causeway, Miami, Florida, matching right and left valves, height 32.9 mm. **q, r**. *C. ornata,* USNM 764717, Plantation Key, Florida, matching right and left valves, height 32.5 mm.

more distinctly pitted microsculpture on the left beak in the pre-radial stage compared to the pattern in the Crassadomini, where there is a complex interplay of discontinuous antimarginal striae, pits, and commarginal lines (Figs. 5, 6).

The new tribe Crassadomini contains only two genera: *Crassadoma* Bernard, 1986, and *Caribachlamys*, new genus.

Crassadoma Bernard, 1986

Original diagnosis.— "Juvenile a typical *Chlamys*, equivalve, biconvex. Right valve ornamented with bifurcating weakly imbricated riblets. Anterior auricle long, with imbricated radial sculpture. Byssal notch deep, ctenolium with six teeth. Posterior auricle small, wide. Left valve with 10 to 15 spinose ribs, separated by three small weakly imbricate riblets. Free or byssiferous. Adult cemented to substrate by right valve. Shell ponderously thickened, irregular, auricles and byssal notch obsolete. Right valve idiomorphic flat or deeply cupped, ornamented with concentric lamellae or with radial rows of imbricated scales. Left valve flattened, with radial rows of imbricated ribs. Hinge line distorted, displaced resulting in large cardinal area." (Bernard, 1986: 72).

Emended diagnosis.— Byssate or cemented Crassadomini with normal prodissoconch (small PI stage and large PII); antimarginal striae absent or weakly developed between commarginal lirae in rib interspaces in early ontogeny; medial intercalation of secondary riblets in rib interspaces recurrent throughout ontogeny of left valve.

Type species.— *Lima gigantea* Gray, 1825, by original designation (Bernard, 1986).

Other species.— *Ostrea pusio* Linnaeus, 1758, extant, eastern Atlantic; *O. multistriata* Poli, 1795, extant, eastern Atlantic; *Chlamys harmeri* Regteren Altena, 1937, Plio-Pleistocene, Europe.

Geographic range.— Eastern Pacific and eastern Atlantic.

Stratigraphic range.— Early? Miocene, Middle Miocene to present. (See following section on the type species, *Crassadoma gigantea.*)

Discussion.— Bernard (1986) included only one species in his new genus, the extant *"Hinnites" giganteus* of the eastern Pacific, and asserted that shell attachment to the substrate in this species evolved independently of the same habit among other extant cementing species (see above discussion of tribe Chlamydini). He also contended that *Crassadoma* is an obligatory cementer, whereas *Hinnites* is only a facultative one, its right valve merely appressed against the substrate, not cemented. Unfortunately, Bernard (1986: 71) misstated the type species of *Hinnites* to be *Hinnites distortus* (DaCosta, 1778) (= *H. pusio)* and gave no information on *H. crispus*, the correct type species. Bernard's (1986) diagnosis of *Crassadoma,* quoted above, is merely a description of the type species and does not serve to differentiate this from other genera that may or may not assume a cemented life habit. Harper (1991: 193) found that although some specimens of *"Hinnites" pusio* may be uncemented and merely wedged into the substrate by their irregular growth, the cemented forms are cemented in the same manner as *Crassadoma* and other *"Hinnites".*

In the present study, the concept of *Crassadoma* is expanded to encompass both non-cemented and cemented Crassadomini that have a plesiomorphic normal prodissoconch (small PI and large PII stage, Fig. 5). This prodissoconch morphology distinguishes *Crassadoma* from the contribal new genus *Caribachlamys,* all species of which share a derived state of the prodissoconch (large PI and small PII stage, Fig. 7). The two genera also differ in the development of antimarginal striae between the commarginals. In *Crassadoma* these striae are obscure or absent (Fig. 5); in *Caribachlamys* they are strong (Figs. 7i, j) and in the more derived species cause the commarginal lirae to assume irregular trends (Fig. 7l). Cemented species of *Crassadoma* are well separated on the basis of the macro- and microsculpture of the *Chlamys* stage from other *"Hinnites"*, most of which fall within the tribe Chlamydini (see preceding discussion of the tribe Chlamydini).

Evidence from the fossil record suggests that cementation in the Crassadomini has evolved independently and at different times in *Crassadoma gigantea* of the eastern Pacific and in *C. pusio* of the eastern Atlantic (see following sections on species). Like all cemented Chlamydinae, these species display changes in morphology resulting from cementation and growth in a confined space, including ventral migration of the ligament system and increased distance between the pallial line and the shell margin (Yonge, 1951; Waller, 1972, 1991; Harper, 1991). Like many species adapted to cooler waters, whether cemented or not, these cemented species have a prominent transgression of foliated calcite ventrally across the originally aragonitic region of the umbonal interior. These are features that occur in each independent origin of *"Hinnites"*, including the two examples of cemented species in the Chlamydini described above. A foliated-calcite transgression has also evolved in many species in other clades both within and outside of the subfamily Chlamydinae (Waller, 1991; Waller and Marincovich, 1992).

Crassadoma gigantea (Gray, 1825)

(Figs. 5c, f, i, 6a, b)

Lima gigantea Gray, 1825: 139. No locality specified.

Hinnita giganteus Gray, 1826: 103.

Pecten (Chlamys) multirugosus Gale, 1928: 92. New name for *Hinnita gigantea* Gray.

Refer to Grau (1959: 134) and to Roth and Coan (1978) for details of synonymy and nomenclature.

Types.— The holotype of *Lima gigantea* Gray, 1825, which Grau (1959: 136) said is in the British Museum (Natural History), was not examined.

Type locality.— "Juan de Fuca Strait (between Vancouver Island, British Columbia, Canada, and the state of Washington, U.S.A." (Grau, 1959: 136).

Diagnosis.— Cemented *Crassadoma*; left valve with scaly radial ribs of at least three orders, with total number of ribs of all orders exceeding 100 at distal margin in mid-ontogeny; rib number commonly decreasing in late ontogeny due to disappearance of lower order riblets; first and second order ribs of left valve remaining distinctly higher in relief than intervening lower order riblets in mid-ontogeny; right valve with fasciculated radial ribs in early ontogeny and at least two orders of ribs in mid-ontogeny; interior of shell vivid purple in color on auricles and hinge plate, foliated calcite transgression extensive, completely covering area inside of pallial line except for muscle scars.

Morphological variation.— During the *Chlamys* stage of ontogeny of *"Hinnites"*, before cementation to the substratum by the right valve, shell attachment is by means of a byssus, with the right valve having a deep byssal notch, well-developed ctenolium (Waller, 1984), and uniform shell curvature. At the end of this stage the mantle of the right valve loses its structural integrity and begins to conform to the substratum surface. Regular sculpture disappears where cementation occurs, but sculptural patterns return whenever the mantle lifts away from the substratum. In *Crassadoma gigantea,* the shell height of the *Chlamys* stage (Figs. 6a, b) varies from about 15 to 30 mm even within population samples (e.g. USNM 764937, Newport Beach, California). Although no geographic trends in maximum size were noted among specimens examined, Hertlein (1972: 212) indicated that size increases northward. The largest specimen that I observed is from Alaska (USNM 678351, Prince of Wales Island, ht. = 24 cm), but Hertlein (1972, p. 212) mentions a "huge specimen" of 23 cm shell height from Santa Cruz Island, California. Shell thickness and the degree of ventral migration of the ligament system are both strongly correlated with size. Extreme ventrad ligament migration produces large ligament areas and a resilium that is much higher than long.

Comparison.— *Crassadoma gigantea* differs from its cemented congener of the eastern Atlantic, *C. pusio* (see below), in being of much greater maximum size and in having more prominently fasciculated ribs on its right valve and more distinctly ordered ribs on its left (compare Figs. 6a, b with Figs. 6k, l). The vivid purple color present on the hinge plate of *C. gigantea,* particularly on the left valve, is absent or faint in *C. pusio*. Although it is generally assumed that *C. gigantea* is thicker shelled than is *C. pusio*, it is doubtful that there is any significant difference when size is taken into account. Both *C. gigantea* and *C. pusio* have extensive development of foliated calcite inside the pallial line, and in both species the crossed lamellar aragonite that is present in this region in early ontogeny is covered over by foliated calcite earlier on the left valve interior than on the right, a common phenomenon among pectinids. *C. gigantea* is more derived than *C. pusio* in the sense that the foliated calcite transgression begins earlier in ontogeny, appearing on the umbonal interior of right valves as small as 11 mm in shell height and on left valves as small as 7 mm. In *C. pusio* it has been observed in right valves no smaller than 17 mm and on left valves no smaller than 13 mm. In *C. multistriata* the plesiomorphic condition persists; there is no foliated calcite transgression over the umbonal interiors at any stage of ontogeny.

Adegoke (1969: 103) described a new species of *"Hinnites", Hinnites benedicti* Adegoke, 1969, from the Late Miocene Santa Margarita Formation of California. Although this species was found in the same beds as *H. multirugosus crassiplicatus* (Gale, 1928) [= *Crassadoma gigantea*], Adegoke regarded it as distinct because of its larger *Chlamys* stage and more even ribbing. My own examination of Adegoke's types at UCMP confirmed this distinctness but did not confirm that *"Hinnites" benedicti* has a cementing habit. The maximum size of the *Chlamys* stage (34 mm) given by Adegoke is exceeded by the height of the holotype (46.8 mm) and two of the paratypes, none of which show any evidence of cementation. The holotype, a right valve, would be expected to show an abrupt sculptural change and xenomorphic growth if cemented. Instead, the degree of shell irregularity is comparable to that of extant *Laevichlamys irregularis* of the Indo-Pacific, a species with a byssate, nestling living habit. The style of ribbing of *H. benedicti* and the apparent lack of commarginal lirae suggest that it is not a *Crassadoma*, but its generic assignment awaits examination of better preserved material. Most likely it is a *Chlamys, s.s.* on the basis of its style of ribbing introduction.

Living habits.— From just below low tide level to 80m (Hertlein, 1972: 212; Grau, 1959: 137; Bernard, 1983: 25); attached to rocks, coarse gravel, and other hard objects. Specimens in northern waters tend to live closer to shore and at shallower depths than those in southern waters (Hertlein, 1972: 212).

Geographic range.— Aleutian Islands, Alaska, to Bahía Magdalena, Baja California, Mexico; offshore in Santa Barbara Islands, California, Guadalupe Island, Mexico (Grau, 1959: 137), and Islas de Revillagigedo, Mexico (reported herein, CAS 60266).

Stratigraphic range.— Early Miocene?, Middle Miocene to present.

The presence of *Crassadoma gigantea* in the Middle Miocene through Pleistocene of California is apparently well established (Moore, 1984: 66). Lower Miocene records, however, are few in number and could require reexamination. The only Lower Miocene record listed by Moore (1984: 66) is from the Painted Rock Member of the Vaqueros Formation. Arnold (1906: 94) also listed a single occurrence, "associated with *Turritella hoffmanni*" in rocks that he referred to as Lower Miocene. Smith (1991a: 35), in reviewing the changing concepts of the age of the "Vaqueros Stage", pointed out that some records in faunal lists need redetermination and further collecting to determine stratigraphic position. The earliest reliable records in California appear to be from the "Margaritan Stage", which Smith (1991a, figs. 12, 14) shows as ranging from planktic foraminiferal zone N12 into lower N16 (Langhian into lower Tortonian stages of Europe) and as correlating with the Shoal River and Yellow River Formations of Florida.

Discussion.— Previous workers (e.g. Grant and Gale, 1931: 161; Waller, 1991: 23) have assumed that *Crassadoma gigantea* evolved from a member of the *Chlamys* group, e.g. *Chlamys hastata,* within the eastern Pacific. For reasons given above, however, this is unlikely. *C. hastata* and its congeners in the eastern and northern Pacific have features that place them squarely within the tribe Chlamydini as herein defined, whereas *C. gigantea* has a microsculptural pattern shared with the other species placed here in the tribe Crassadomini. Specifically, in the early ontogeny of *C. gigantea* the plesiomorphic pattern of continuous sweeping antimarginal striae is absent and commarginal lirae are prominent in rib interspaces (Fig. 5f).

Crassadoma gigantea has a ribbing pattern that is more derived in comparison to the patterns of its eastern Atlantic congeners, and its large size and purple hinge also are derived in comparison to the eastern Atlantic species and to outgroup Chlamydinae. Given the absence of *Crassadoma* in the Indo-west Pacific, it is highly likely that *C. gigantea* evolved from species that were present in the Atlantic. There remains the problem, however, of where the fossils are which should corroborate this ancestry. If it is true that *C. gigantea* was already present in the eastern Pacific by the middle Miocene, it is likely that an ancestor was present in the western Atlantic and that it dispersed through seaways to the Pacific at this time or earlier. If the ancestral species was eurytopic with a preference for warm temperate but not strictly tropical temperatures, it is possible that it avoided the shallow water habitats that predominate in the early Miocene stratigraphic sections thus far known in the Caribbean. The absence of these fossils thus could be the result of a facies sampling bias in the region in which they are most likely to be found. The most likely interval of the middle Miocene for speciation to have occurred may have been during the time of initial emergence of the Isthmus of Panamá. This uplift cut off the flow of intermediate water between the Atlantic and Pacific and intensified the southward flow of the cool California Current along the Mexican coast, creating a thermal barrier to the west-to-east dispersal of shallow water taxa (Duque-Caro, 1990).

Material examined.— Recent material: USNM: 90 lots containing about 150 specimens, from Baja California, Mexico, to Alaska.

Fossil material: USNM: about a dozen lots containing fewer than 20 specimens, Miocene (Santa Margarita Formation) to Pleistocene, from Baja California, Mexico, and California.

Crassadoma multistriata (Poli, 1795)

(Figs. 5a,d,g; 6c-j)

Ostrea multistriata Poli, 1795: 164, pl. 28, fig. 14, living, Sicily.

Pecten tinctus Reeve, 1853, species 106, pl. 26, fig. 106, living, locality unknown.

Pecten effulgens Reeve, 1853, species 156, pl. 33, fig. 156, living, locality unknown.

Pecten textilis Reeve, 1853, species 174, pl. 35, fig. 174, living, locality unknown.

Pecten multistriatus (Poli), Bucquoy *et al.*, 1887: 104. Gives extensive synonymy.

Chlamys multistriata (Poli), Roger, 1939: 165. Gives extensive synonymy.

Types.— Poli's (1795) work on the living bivalves of Sicily was based largely on his own extensive shell collection (Dance, 1966: 95; Kohn, 1988: 39), which apparently has not been preserved. Previous authors who have discussed the taxonomy of this well-known species in detail, e.g. Bucquoy *et al.* (1887: 104), Sacco (1897: 6), and Roger (1939: 165), have not mentioned type specimens, possibly because Poli provided an illustration the identity of which has never been questioned. Following the International Code of Zoological Nomenclature [Art. 74(b)] and the example of Kohn (1988: 39), the specimen represented by the figure in Poli (1795, Pl. 28, Fig. 14) is herein selected as the lectotype.

The types of the three species of Reeve (1853) listed in the synonymy were examined at The Natural History Museum, London. All are represented by syntype series. In the interest of nomenclatural stability, lectotype designations are as follows:

Pecten tinctus Reeve, syntypes, two complete shells and a single right valve. The specimen of height 32.5 mm, length 27.5 mm, and convexity of the complete shell 13.0 mm, BMNH 1981247/1 is herein selected as the lectotype (Figs. 6e,f), because it is apparently the specimen that Reeve figured. The paralectotypes are BMNH 1981247/2-3.

Pecten effulgens Reeve, syntypes, two complete shells. The darker of the two, BMNH 1993039/1, height 18.8 mm, length 15.0 mm, is represented in Reeve's figure 156 and is herein selected as the lectotype (Figs. 6g,h). This taxon was recently incorrectly placed in the synonymy of *P. cruentatus* Reeve, 1853, by Rombouts (1991: 27). Reeve's *P. cruentatus* is a Mimachlamys that is closely related to and possibly a junior synonym of the Indo-Pacific *Mimachlamys senatoria* (Gmelin, 1791).

Pecten textilis Reeve, syntypes, a single right valve (Fig. 6j) and single left valve (Fig. 6i). The left valve, BMNH 1993040/1, height 24.9 mm, length 20.2 mm, is represented in Reeve's fig. 174 and is selected herein as the lectotype.

Type locality.— Sicily.

Diagnosis.— Byssate, non-cemented *Crassadoma* of small size (less than 40 mm in height); ribs introduced continuously throughout ontogeny without distinct clustering or ordering; 70 to 80 continuously scaly ribs and riblets present at distal margin of mature shells; inner surface of shell inside pallial line lacking foliated calcite throughout ontogeny.

Morphological variation.— The only significant geographic variation in *Crassadoma multistriata* occurs along the Atlantic and Indian Ocean coasts of southern Africa, where specimens tend to have narrower umbonal angles (as narrow as 80°) and correspondingly higher height to length ratios (as high as 1.34). Some authors have considered these narrow forms to be a distinct species, *Chlamys tincta* (Reeve, 1853) (Figs. 6e,f). The two forms, however, overlap in shell narrowness and are identical in details of ribbing and microsculpture.

Some authors have thought that *Crassadoma multistriata* becomes cemented in the northern part of its range along the Atlantic coast of France and have therefore treated this species and *C. pusio* as synonyms (see following discussion). On the basis of the evidence on hand, however, I have not been able to substantiate intergradation of these taxa. Bucquoy *et al.* (1887: 104) noted the presence of both regular and distorted forms in single samples from Brest, France, but illustrated a regular specimen that was still within the size range of the pre-cementation stage of *C. pusio.* Shell distortion in the absence of cementation is not a diagnostic feature, because it occurs in many independent lineages of byssate, nestling chlamydoid pectinids. In *C. multistriata,* distortion is common among many specimens in the Atlantic, including specimens at both the northern and southern limits of its geographic range. Pre-cemented *C. pusio,* however, can generally be distinguished from *C. multistriata* in the same size range using criteria summarized below.

Comparison.— *Crassadoma multistriata* (Figs. 6a-j) closely resembles its western Atlantic counterpart, *Caribachlamys sentis* (Figs. 6m-p), in shell shape, color, and the lack of a foliated-calcite transgression on the inner shell surface in the umbonal region. The former, however, has a normal prodissoconch (Fig. 5a), whereas that of the latter has a prodissoconch dominated by the PI stage (Figs. 7a,g). The umbonal region of the disk of *C. multistriata* is more inflated and less flattened than that of *C. sentis,* and the byssal fasciole of *C. multistriata* generally has a deeply incised groove whereas that of *C. sentis* does not.

Crassadoma multistriata differs from *C. pusio* (Figs. 6k,l) in lacking cementation and foliated-calcite umbonal transgressions throughout ontogeny. In *C. pusio* cementation and attendant changes in morphology begin at shell heights between about 12 and 25 mm. The pre-cementation growth stage of *C. pusio* closely resembles shells of *C. multistriata* of similar size. Even at this early stage, however, the two species can be distinguished by two features. First, in *C. multistriata*, there is no transgression of foliated calcite from the hinge region ventralward across the region inside the pallial line at any stage of growth. In *C. pusio*, foliated calcite generally begins to form on the inner shell surface at the dorsal edge of the umbonal region at a shell height of about 17 mm in right valves and about 13 mm in left valves, generally before cementation begins. In mature shells over most of the geographic range of *C. pusio,* this foliated calcite may extend ventrally at least to the level of the top of the adductor scar. Secondly, the beak of the left valve of *C. multistriata* has only weak microsculpture, particularly near the distal margin of the preradial stage (Fig. 5d); microsculpture at this same stage is stronger in *C. pusio,* consisting of distinct, generally discontinuous antimarginal striae and pits (Fig. 5e).

Crassadoma multistriata also resembles *C. harmeri* (Regteren Altena, 1937) of the Plio-Pleistocene of western Europe and Great Britain. The fossil species differs in reaching a larger size (commonly exceeding a height of 70 mm), in having a minor foliated-calcite transgression on the inner shell surface in the umbonal region of each valve, and in having a distinct anterior-posterior trending ridge on the inner surface of its right anterior auricle.

Living habits.— *Crassadoma multistriata* lives byssally attached to hard objects on the substrate at shallow shelf depths from below low tide level to at least 100 m in normal marine environments. Dead shells, particularly of juveniles, have been dredged from depths as great as 700 m. The species is apparently eurythermal and possibly has been ecologically generalized throughout much of its history. Blondel and Demarcq (1990: 250), in a study of the Early and Middle Miocene (late Burdigalian to early Langhian) fossil record of northern Tunisia, refer to the species as eurytopic.

Geographic range.— *Crassadoma multistriata* has an enormous latitudinal range, occurring from the Brittany coast of France southward into the Mediterranean and thence southward along the African coast to southernmost South Africa (Nicklès, 1955). The species occurs throughout the Mediterranean as well as in the Madeira, Canary, and Cape Verde Islands. It is also present in the central South Atlantic at St. Helena (USNM 124060 and 764331). Along the southern and southeastern coasts of Africa, *C. multistriata* is abundantly represented in USNM collections from False Bay, South Africa, to southern Mozambique (USNM 764201 and 764219) in the Indian Ocean.

Stratigraphic range.— Lower Miocene to present.

Sacco (1897: 9) showed the stratigraphic range of *"Chlamys" multistriata* as extending as far down as the Tortonian (Upper Miocene) and that of its lineage antecedent, *"Chlamys" tauroperstriata* Sacco, 1897, *sensu stricto,* as extending as far down as the lowermost Miocene (Aquitanian). Cox (1927: 42-43) thought that *"Chlamys" pusio* (which he used as a senior synonym of *Chlamys multistriata*) was "well established in Lower Miocene times" and was present in the Miocene of Persia. Roger (1937: 167) noted that *"Chlamys" multistriata* is common in the Lower Miocene (Burdigalian) in the Mediterranean region from the Rhône Valley to the Vienna Basin. It is generally thought that the species has a Mediterranean origin (Lauriat-Rage, 1981: 43). The stratigraphic history of the species in the eastern Atlantic outside of the Mediterranean, however, is not precisely known.

Discussion.— The discrimination and nomenclature of *Ostrea multistriata* Poli, 1795, and *O. pusio* Linnaeus, 1758, have long been contentious issues in pectinid taxonomy. Many authors, e.g. Jeffreys (1863: 52), Bucquoy *et al.* (1887: 107-108), Dautzenberg and Fischer (1925), and Roger (1939: 166), have considered the two species to be intergradational, with cementation absent throughout the ontogeny of Mediterranean specimens but variably present or absent in the later ontogeny of specimens living in the Atlantic. If intergradation in fact exists, then clearly the two names should be synonymized, and one would normally expect the name with priority, *O. pusio,* to apply to both. Many authors (Bucquoy *et al.*, 1887: 104; Sacco, 1897: 7; Roger, 1939: 165), however, have pointed out that the Linnaean name is poorly founded, not only because of the generalized brief description given by Linnaeus, but also because the species is not represented by a clearly isolated specimen in the Linnaean Collection. These authors have therefore discarded the name *O. pusio* and have elected to use Poli's name *multistriata* instead, applying the name *Chlamys multistriata* to both byssate and cemented forms. In so doing, these authors have ignored the priority of *Pecten distortus* Da Costa, 1778, as well as the possible validation of Linnaeus's name by Pennant (1777), who provided an excellent illustration. Da Costa's name has been used extensively by British malacologists for the cementing form, which is the only form known to be present in British waters.

If the only criterion for distinguishing *Crassadoma multistriata* from *C. pusio* is the presence of cementation in the advanced growth stages of the latter, then cementation itself cannot be used to settle the problem of intergradation, because its presence becomes a circular argument for the discrimination of the two species. On the basis of the two characters discussed in the preceding comparison (the extent of the foliated-calcite transgression on the inner shell surface and the degree of coarseness of left beak sculpture), I was unable to find evidence of intergradation in the extensive eastern Atlantic Jeffreys Collection (USNM). The position taken in the present study, therefore, is that the cementing and non-cementing forms of *Crassadoma* in the eastern Atlantic are distinct species which, for reasons of priority, must retain the names *C. pusio* and *C. multistriata,* respectively. The issue of the type specimen of *C. pusio* is treated in the following section.

Material examined.— Recent material: USNM: 73 lots containing about 300 specimens, mainly Mediterranean (Spain, France, Italy, Yugoslavia, Turkey, Tunisia, Algeria) but also eastern Atlantic off Africa (Cape Verde Islands, Guinea-Bissau, Senegal, Angola, Namibia), Indian Ocean (off southern Mozambique), and central Atlantic (St. Helena). In addition to the type specimens discussed above, numerous non-type lots were examined at museums in Great Britain and Europe, particularly at BMNH, BRM, AM, LM, and ZMC.

Fossil material: Numerous specimens at BMNH, BRM, UCBL, and TUI.

***Crassadoma pusio* (Linnaeus, 1758)**

(Figs. 5b,e,h, 6k,l)

Ostrea pusio Linnaeus, 1758: 698, no. 169, living, in "O. australiore."

Pecten pusio (Linnaeus). Pennant, 1777, pl. 61, fig. 65, living, Great Britain.

Pecten distortus Da Costa, 1778: 148, pl. 10, figs. 3, 6, living, England and Scotland (Orkneys).

Ostrea sinuosa Gmelin, 1791: 3319, living, in British seas.

Pecten spinosus Brown, 1827, pl. 33, fig. 8, living, Northumberland coast, England [name and figure only]; Brown, 1844: 73 [description, with 1827 figure repeated].

Pecten crotilus Reeve, 1853, species 150, pl. 33, fig. 150, living, locality unknown.

Type specimens.—In the Linnaean Collection at the Linnaean Society, London, the pair of matching valves of a distorted and cemented *"Chlamys"* present in the tray bearing Collection Sequence No. 179, with height 37 mm and length 35mm, is herein designated the lectotype of *Ostrea pusio* Linnaeus, 1758. The background and basis for this designation are given in the following discussion.

The type or types of *Pecten distortus* Da Costa, 1778, have not been examined nor has their depository been determined. Dance (1966: 283) reported that some Da Costa types are in The Natural History Museum, London, and some are in the Glasgow University Museum. Ms. Kathie Way, Collections Manager at BMNH (Invertebrates I), reported that no type material for *P. distortus* has been found there (pers. comm., 1993).

The type series of *Pecten crotilus* Reeve, 1853, BMNH 1993042, consists of four specimens mounted on a board in the Cuming Collection in The Natural History Museum (London). I examined these and determined that they are young *Crassadoma pusio.*

Type locality.— Herein specified as northeastern Atlantic.

Diagnosis.— Cemented *Crassadoma* of moderate size (uncommonly greater than 60 mm in height); ribs introduced continuously throughout ontogeny without distinct clustering or ordering; 60 to 80 ribs and riblets present at distal margin of mature shells; inner surface of valves with small foliated-calcite transgression in umbonal region, seldom extending past level of dorsal edge of adductor in mature shells.

Morphological variation.— The height of right valves at the time of their cementation to the substratum varies from about 12 to 25 mm. There is no evidence in the collections examined for geographic changes in the height at first cementation or in the frequency of cementation within samples. In general, all individuals within populations of *Crassadoma pusio* seem to become cemented after a certain stage of ontogeny is reached. Harper (1991: 192), however, found that some individuals remain uncemented and merely become lodged into the substratum by means of their irregular growth form. The presence of small foliated-calcite transgressions in the umbonal region of both valves is fairly consistent, again without observed geographic trends. Some exceptional specimens (USNM 543396) collected from floating mines and buoys off the Atlantic coast of Morocco, however, lack foliated calcite in the umbonal region even at a shell height of 36 mm, well past the stage of initial cementation. A foliated-calcite transgression is present, however, in a specimen from deeper water off Morocco (USNM 196510, 132-234 m) and in a specimen from 90 m off Ivory Coast (USNM 764327). All of these specimens have coarse microsculpture in the pre-radial stage of the left valve like that of more typical *C. pusio.*

Comparison.— The pre-cemented growth stage of the shell of *Crassadoma pusio* closely resembles the shell of *C. multistriata* of a similar size. Refer to the preceding section on *C. multistriata* for comparative details. *C.pusio* differs from other cementing *"Hinnites"* of the eastern Atlantic in being of smaller maximum size and having less extensive foliated calcite inside the pallial line. Both *Hinnites corallinus* and *Chlamys ercolaniana* (see above) lack the prominent commarginal lirae that are present between ribs in the early ontogeny of *C. pusio.* The early *Chlamys* stage of *H. corallinus* differs from those of the other two cementing species in having ribs that begin late, following an extensive pre-radial area having antimarginal striae in a uniform sweeping pattern. The *Chlamys* stage of *Chlamys ercolaniana* differs from that of *C. pusio* in having a distinctive microsculpture in rib interspaces. This consists of antimarginal striae of highly irregular trends, probably a vestige of the shagreen microsculpture present in the ancestry of this species. Contrary to a statement by Harper (1991: 190), *C.*

pusio lacks shagreen microsculpture. The microsculptural pattern that she interpreted to be shagreen (her fig. 4.4) is a typical plesiomorphic pattern of antimarginal striae.

Living habits.— The early growth stage of *Crassadoma pusio* is byssate on hard objects, particularly rocks or shells, later becoming cemented by the edges of the right valve to the same substratum. Depth records for specimens collected alive range from just below low tide level to about 100 m. Jeffreys (1863: 52) reported that the species lives in depths from 5 to 85 fm (9 to 155 m), with only young specimens found near or in the tidal zone.

Geographic range.— Common throughout the British Isles from the Orkney Islands to Cornwall and extending across the North Atlantic as far westward as southwestern Iceland (Madsen, 1949: 30); present along European coasts from northern Norway (69° 22.5'N, Soot-Ryen, 1951) southward to Spain and Portugal; uncommon on African coast from Morocco to Ivory Coast; present in Azores; apparently rare in the westernmost Mediterranean.

Stratigraphic range.— Pleistocene? to present.

The common tendency for authors to combine cemented and non-cemented *Crassadoma* in a single species referred to as either *Chlamys pusio* or *C. multistriata* makes it difficult to tabulate stratigraphic occurrences from the literature when the presence of cementation is not specified (e.g. Sacco, 1897; Roger, 1939; Eames and Cox, 1956). Roger (1939: 167) noted that fossils with the form of *C. distorta,* presumably meaning cemented forms, are quite rare in the fossil record of the Mediterranean but occur in the Pliocene of France. Apparently the only cemented pectinid in the Pliocene Coralline Crag of Great Britain is the gigantic form that Wood (1861: 19) referred to as *Hinnites cortesyi* De France, 1821. Roger (1939) considered the latter to be a junior synonym of *H. crispus.* Indeed, Wood's superb illustration leaves little doubt that this is a true *Hinnites* and not a *Crassadoma* (see above). Fossils that Wood (1861: 33) determined to be *"Pecten pusio,* Pennant" are also present in the Coralline Crag as well as the younger Red Crag. These shells, as noted by Wood (1861: 34), are not cemented and retain their shell regularity to large size (greater than 50 mm). Specimens of these that I examined can be identified with *Crassadoma harmeri* (Regteren Altena, 1937), which Glibert and Van de Poel (1965: 34) consider to be a subspecies of *"Mimachlamys" multistriata* (Poli). If these fossil *Crassadoma* are ancestors of true *C. pusio,* it is possible that the modern cemented form that is so common in British waters originated within the Pleistocene and possibly very late in the Pleistocene. Harper (1991: 197), who studied the phenomenon of cementation among many bivalve clades, also concluded that cementation in this species has a post-Pliocene origin.

Discussion.— Malacologists have long acknowledged that the original description of *Ostrea pusio* by Linnaeus is too generalized to be useful and that the lot in the Linnaean Collection bearing this name contains shells belonging to more than one species. In the first detailed study of the Linnaean Collection after Linnaeus's death, Hanley (1855) reported that the marked receptacle bearing the name *O. pusio* in the collection "has unfortunately been converted into a general depository for all the loose valves of the smaller *Pectens*...." He acknowledged, however, that the box contained shells belonging to "the *pusio* of the British writers and the *albolineatus* of Sowerby's [1842] Monograph," as well as a "white valve of the young *Islandicus.*" He conjured that Linnaeus's ill-fitting description may have been of a composite consisting of the valves of different species. He concluded, however, that the species then known to British writers as "*P. sinuosus* (= *pusio*) ...(of which there are many loose specimens in the cabinet) accords the best with the definition..."

This conclusion did little to resolve the problem of a type for *Ostrea pusio*, and in subsequent years Linnaeus's name, as well as the names *Pecten distortus* Da Costa, 1778, and *O. sinuosa* Gmelin, 1791, have all been used for the cemented pectinid of the northeastern Atlantic. Cox (1927: 43), adamantly defending the use of Linnaeus's name but applying it to both the cemented form of the Atlantic and the byssate form of the Mediterranean, said that he would propose "a definite specimen from the Linnaean Collection and figure it as the lectotype of the species." However, I can find no record that he ever did so. Dodge (1952: 178), in a later study of the Linnaean Collection, added nothing new to the findings of Hanley (1855). He urged retention of Linnaeus's name, however, because of its extensive use, particularly by writers in the last half of the nineteenth century. Glibert and Van de Poel (1965: 33) followed Dodge's advice, but noted further that even if *O. pusio* of Linnaeus be regarded as an unacceptable name, *P. pusio* Pennant, 1777, which applies to the British cemented species, is available and has priority over *O. multistriata* Poli, 1795 (and also over *P. distortus* Da Costa, 1778, and *O. sinuosa* Gmelin, 1791). Wallin (1991: 154), who reported on the contents of the Queen Ulrica Collection (which contains material that may have been examined by Linnaeus prior to the publication of his tenth-edition names in 1758) found specimens of *O. pusio* to be present. My own examination of the Linnaean Collection at the Linnaean Society in London in 1977 found that the tray labeled in Linnaeus's hand as *O. pusio* contains four specimens: a pair of matching valves of cemented *Crassadoma pusio,* height 37 mm, length 35 mm, with approximately 40 radial ribs (secondary ribs not counted); a pair of matching valves of *Mimachlamys albolineata* (G.B. Sowerby II, 1842); a single left valve of *M. albolineata;* and a single juvenile right valve of *Chlamys islandica* (Müller, 1776).

Dance (1967: 8) urged that caution is necessary when designating types from the Linnaean Collection because of the checkered history of the specimens in the collection, which now includes non-Linnaean material. In the case of *Ostrea pusio*, however, it seems likely that specimens of this common species of the northeastern Atlantic were available to Linnaeus, as indicated by their presence in both the Linnaean and Queen Ulrica Collections. In view of the long history of usage of the name, the above designation of a lectotype from the Linnaean Collection seems to be justified.

Material examined.— Recent material: USNM: 55 lots containing about 250 specimens, mainly from Great Britain but including material from Sweden, France, the Azores, Morocco, and the Ivory Coast. In addition, numerous specimens were examined in the collections abroad, mainly at BMNH, BRM, MNHN, AM, LM, and ZMC.

Fossil material: No unequivocal cemented *Crassadoma pusio* were found among material examined at museums abroad, underscoring the apparent late origin of this cemented species. At the time of my European studies, however, the ontogenetic criteria for differentiating *C. pusio* and *C. multistriata* had not yet been discovered.

Caribachlamys Waller, new genus

Etymology.— The name *Caribachlamys* combines a prefix signifying Caribbean with the genus name *Chlamys.*

Diagnosis.— Byssate, non-cemented Crassadomini with lecithotrophic-type prodissoconch (large PI stage, short or absent PII stage); strong antimarginal striae present between commarginal lirae in rib interspaces in early ontogeny.

Type species.— *Pecten sentis* Reeve, 1853.

Other species.— *Pecten ornatus* Lamarck, 1819; *Caribachlamys paucirama* Waller, new sp.; *Pecten (Chlamys) imbricatus mildredae* Bayer, 1941; *Ostrea imbricata* Gmelin, 1791.

Geographic range.— Caribbean Sea and adjacent waters of the warm-temperate to tropical western Atlantic from North Carolina to Brazil and Bermuda.
Stratigraphic range.— Upper Pliocene to Recent.

Discussion.— The new genus *Caribachlamys* is based on the discovery that four extant species of the Caribbean and adjacent waters share a unique prodissoconch morphology (Figs. 7a-f) and a unique pattern of commarginal and antimarginal microsculpture in rib interspaces (Figs. 7g-l). The phylogenetic relationships of these extant species and one new extinct species are shown in Figure 8. *Caribachlamys ornata* (Node B, Fig. 8) resembles *C. sentis* very closely in ribbing pattern but differs in developing smooth-crested scaleless ribs that are I-beam shaped in cross-section. In the Bahamas the two species nearly intergrade in that specimens identified herein with *C. ornata* develop I-beam shaped ribs only in very early ontogeny and otherwise resemble *C. sentis* (see following section on *C. ornata*). *C. paucirama, C. mildredae,* and *C. imbricata* have ribs that have a plesiomorphic rounded cross-sectional shape (not I-beam shaped) like that in the likely stem species, *C. sentis,* meaning that it is unlikely that *C. ornata* can have given rise to any other species in the genus. *C. paucirama, C. mildredae,* and *C. imbricata* are united (Node C, Fig. 8) by decrease in prominence of the early commarginal lirae in rib interspaces and by the onset of substantial irregularity in the trends of these lirae. At Node D, *C. paucirama* develops an autapomorphy: rib introductions beyond a shell height of 20 mm are few in number or absent altogether, leading to a pattern of ribs of fairly uniform height and spacing at the distal margin. *Caribachlamys mildredae* and *C. imbricata* (Node E) share fasciculation of ribs, increase in scale spacing on major ribs, a tendency toward cusping of scales, and marked flattening of the left disk. Finally, *C. imbricata* (Node F) has evolved a unique ribbing pattern consisting of 9 or 10 major plicae with a tendency for secondary ribs to be eliminated. The scales on the ribs of this species commonly form closed knobs, the left disk is markedly flattened, and the maximum observed irregularity and inconsistency in direction of the early commarginals is reached.

Caribachlamys sentis (Reeve, 1853)
(Figs. 6m-p, 7a, d, g, j)

Pecten sentis Reeve, 1853, species 129, pl. 29, fig. 129, living, locality unknown.
Chlamys sentis Reeve, Abbott, 1954: 363, pl. 34a.

Types.— Among Reeve's types in The Natural History Museum, London, are two pairs of matching valves in a single box labeled "*sentis* Reeve." Upon examining these specimens, I found that the larger specimen, which is a deep orange in color, corresponds in dimensions to Reeve's

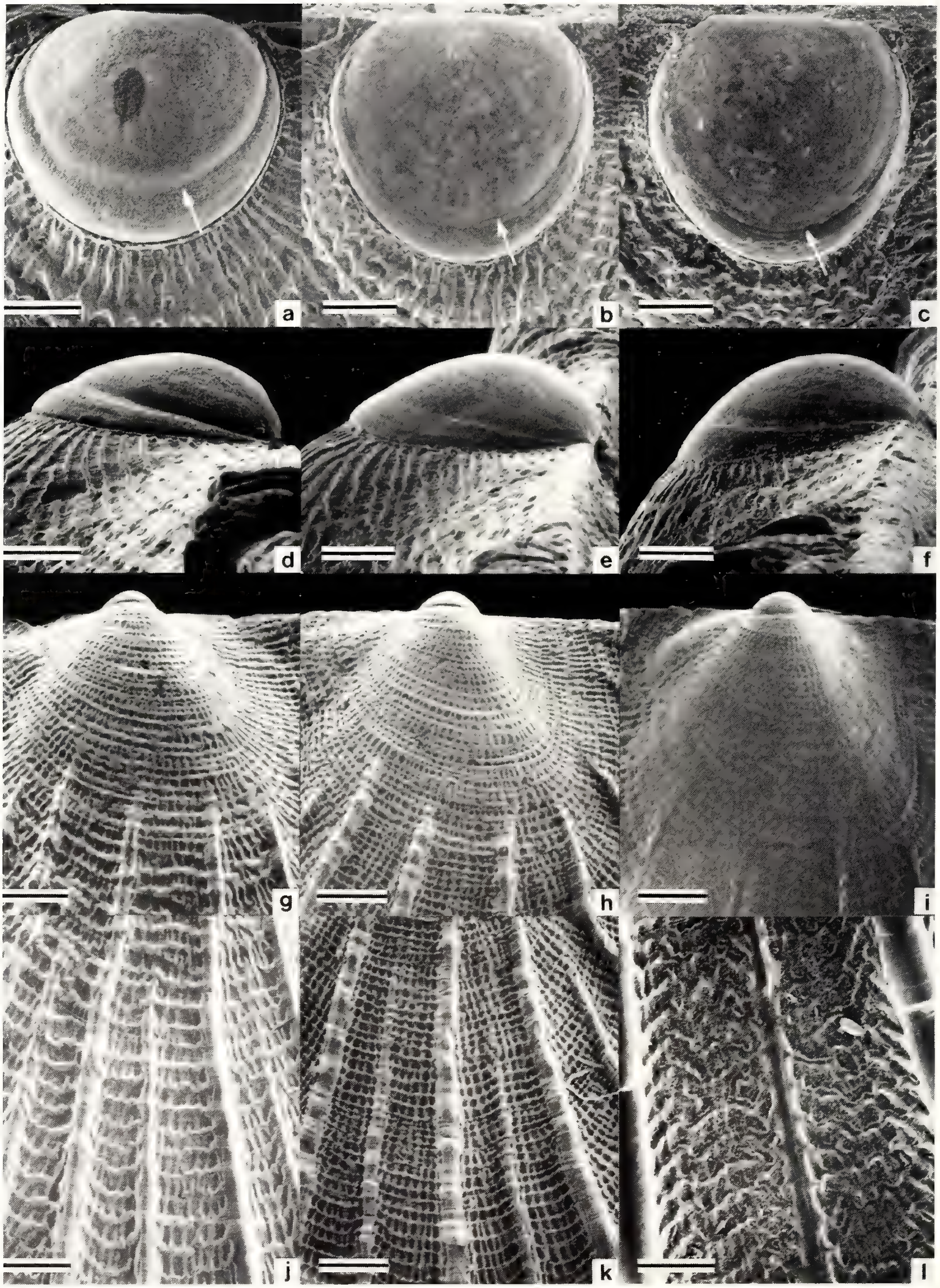

Fig. 7. Scanning electron micrographs of prodissoconchs in planar view (a-c), prodissoconchs in posterior view (d-f), pre-radial microsculpture (g-i), and early radial stage sculpture (j-l) of left valves of *Caribachlamys*. **a, d, g, j**. *C. sentis*, USNM 764706, Molasses Reef, Monroe Co., Florida. **b, e, h, k**. *C. ornata*, USNM 766643, Carrie Bow Cay, Belize. **c, f, i, l**. *C. imbricata*, USNM 457668, Bahia Honda, Cuba. Arrows point to approximate position of PI/PII boundary. Scale bars: a-f = 50 μm, g-l = 200 μm.

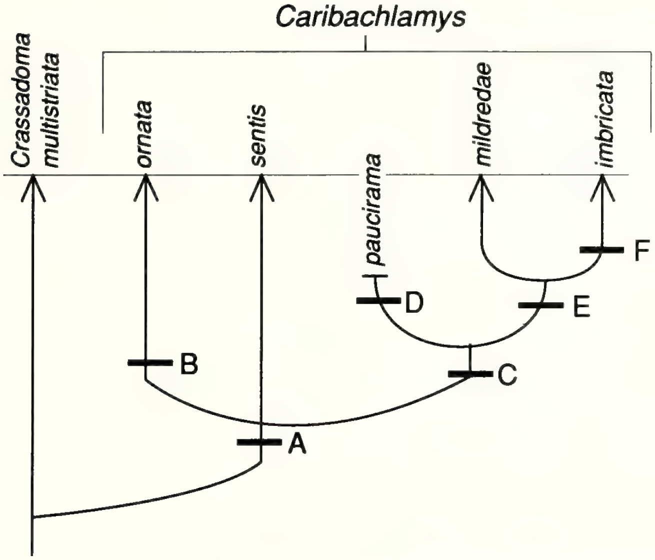

Fig. 8. A phylogeny of species in the new genus *Caribachlamys* in the Plio-Pleistocene of the tropical western Atlantic. Lineages ending in arrows are extant; the one ending at a terminal cross-bar is extinct. Lettered blocks refer to apomorphies: (A) larval shell with large PI and small PII stage; (B) I-beam shaped ribs with smooth crests; (C) subdued commarginal lirae of irregular trend in early ontogeny; (D) rib introductions limited to early ontogeny, later ribs evenly spaced without significant clustering; (E) fasciculation of ribs, increased scale spacing with tendency toward cusping, and flattening of left valve; (F) reduction of ribs to 9 or 10 major plicae with tendency to eliminate secondary ribs, scales commonly forming closed knobs, and left valve markedly flattened.

fig. 125. The smaller specimen, although nearly of the same color, is not the same species but rather is a specimen of *Spathochlamys benedicti* (Verrill and Bush, 1897) (see following section). The larger specimen, BMNH (ht., 15.9 mm; L, 14.3 mm; length of anterior outer ligament, 2.9 mm; length of posterior outer ligament, 0.9 mm) is herein selected as the lectotype (Figs. 6m, n).

Type locality.— Reeve had no locality data for the species that he described. The type locality is herein specified as the western North Atlantic off southeastern Florida.

Diagnosis.— *Caribachlamys* with valves about equal in convexity; ribs closely spaced, fine, continuously scaly, rounded, and of many different heights, introduced continuously throughout ontogeny, with more than 70 ribs and riblets at distal margin of mature individuals; major ribs with straight or slightly undercut sides but not I-beam shaped in cross section; scales fine, closely spaced, erect, distally concave, and open; commarginal lirae well developed in rib interspaces in early ontogeny and fairly uniform in trend across rib interspaces; antimarginal striae prominent between commarginals but variably present on rib crests.

Morphological variation.— *Caribachlamys sentis* is of small size, seldom exceeding a height of 40 mm; no geographic trends in maximum size were observed. The ribs tend to be continuously scaly beginning at their origins at the beginning of the radial stage of growth; there is in general no abrupt change in ontogeny from a non-scaly to a scaly condition. Exceptions occur in the western Caribbean along the coast of Panamá (USNM 743733, Payardi Island, and USNM 743360, San Blas Archipelago). The ribs of the left valves of some of the specimens in these samples lack scales in early ontogeny up to a shell height of from 4.5 to 6.5 mm and then change fairly abruptly to a scaly phase. Unlike the non-scaly phase of ribs in *C. ornata,* however, these ribs have a rounded crest and are not I-beam shaped in cross section.

The shell color and color pattern of *Caribachlamys sentis* are variable. Most commonly, shells are orange or purple with maroon mottling in early ontogeny. In some cases an orange phase may change abruptly along a commarginal growth line to a purple phase, but the reverse has not been observed. Rarely the color may be nearly uniform white or yellow, usually with an early orange-mottled phase.

Comparison.— *Caribachlamys sentis* closely resembles *C. ornata* in ribbing density and pattern. The ribs differ, however, in cross-sectional shape, at least in early ontogeny. In *C. sentis* the rib shape is high and rounded, with the rib crests not flattened, whereas in *C. ornata* the ribs at least in early growth have an I-beam cross-section, with the crests flattened and non-scaly and the rib sides strongly undercut. Specimens from the northern Bahamas identified herein as *C. sentis* are very close to being transitional between the two species in rib shape in early ontogeny. Unworn shells of *C. ornata* have dense antimarginal striae present on the flattened rib crests, whereas in *C. sentis* such rib-crest striae are not so strongly developed. *Caribachlamys sentis* tends to have more uniform coloration than does *C. ornata* and generally does not develop the strongly contrasting color pattern that is common in most *C.ornata*, where dark maroon spots or bars form on a stark white background. *Caribachlamys sentis* and *C. ornata* also tend to differ in living habits. Where the two occur in the same area, *C. sentis* is generally found at more protected sites on reefs, whereas *C. ornata* lives in the more turbulent areas of the reef front.

Caribachlamys sentis also closely resembles *Crassadoma multistriata* (eastern and central Atlantic and southwestern Indian Ocean) in ribbing pattern, color, and color pattern. In *C. multistriata,* however, the prodissoconch is of the normal plesiomorphic type, with a PII stage that is relatively large compared to PI (Fig. 5a); in *C. sentis* the prodissoconch is almost entirely composed of the PI stage, the PII stage being only a narrow fringe or absent (Figs. 7a, d). *C. sentis* also differs from *C. multistriata* in having a somewhat less inflated shell and in generally lacking a distinct groove along the center of the outer surface of its byssal fasciole. Aside from the difference in prodissoconch morphology, young individuals of the two species can be distinguished on the basis of microsculpture. In *C. sentis* the spaces between commarginal lirae of the early commarginal stage are occupied by well-developed antimarginal striae; in *C. multistriata*, antimarginal striae between commarginals are either very poorly developed or absent.

Living habits.— Byssally attached beneath coral heads and between rocks and coral rubble on reef crests in shallow backreef areas, on near-shore rock jetties, and in deeper fore-reef rubble zones; depth range from just below low tide level to about 30 m. Deeper offshore specimens are dead shells only, known to occur as deep as 52 m. Diaz *et al.* (1991), reporting on the molluscan fauna of the Santa Marta area of Colombia, found *Caribachlamys sentis* living in three types of habitats: (1) at a depth of 22 to 27 m at base of the reef front on a bottom of "conglomerates of coral rubble partly bound together by sponges; dead coral heads and scattered debris patches may also be present." (2) at a depth of about 8 to 15m, with the bottom described as "upper reef-slope with large coral heads forming caves and an intricate system of cryptic microhabitats. Species of sea fans, sea whips, and sea plumes are also common." (3) at depths less than 10 m, with the bottom described as "rocky boulders and pebble partly covered by filamentous algae, crusting zoanthids, and fire corals. This zone is present in calm environments in shallow water."

Geographic range.— From Jupiter Inlet, southeastern Florida, southward through the Florida Keys; uncommon in northern, western, and southern Gulf of Mexico [records from Flower Garden Reef, Texas, and off Tamaulipas, Mexico (USNM 764714)]; western Caribbean (Nicaragua, Panamá, Colombia); western Atlantic off Brazil as far south as the state of Santa Catarina (29°S). The presence of the species in southern Brazil is based on Rios (1985: 222); I have not examined these specimens.

Stratigraphic range.— Lower? Pliocene to present.

Discussion.— The only fossil *Caribachlamys sentis* found thus far is a single right valve (USNM(P) 474635) collected by the late S. E. Hoerle from the north side of the Caloosahatchee River, 3.4 km (2.1 miles) west of Ortona Locks, Glades County, Florida. Unfortunately the precise stratigraphic position of this specimen is unknown, because the stratigraphic section at this site likely includes the Caloosahatchee, Bermont, and Ft. Thompson Formations. All that can be said is that it is likely that the specimen is Pleistocene in age.

I have not yet observed unequivocal pre-Pleistocene fossils of *Caribachlamys sentis*, and my estimate of a Pliocene origin is based upon two indirect lines of evidence. First, the oldest fossil member of the tribe Crassadomini in the western Atlantic thus far identified is possibly the specimen figured by Woodring (1925, pl. 7, fig. 10) as *"Chlamys (Chlamys)* sp." from the Bowden Formation (Bowden shell beds) at Bowden, Jamaica. This specimen, USNM(P) 352779, is an abraded juvenile right valve only 4.4 mm in height. Its pattern of rib introduction, by rib-flank intercalation, is remarkably like that at a similar growth stage of *C. sentis* (cf. USNM 764710). The microsculpture of the specimen does not appear to be preserved except for traces of antimarginal striae on the anterior and posterior edges of the disk and disk flanks and some obscure traces of commarginal lirae. The prodissoconch of the specimen is not preserved, but the impression of it remains on the underlying shell material. This impression has a length of 163 µm, exactly the length that one would expect for the prodissoconch of a *Caribachlamys*. The prodissoconchs in species of *Crassadoma* are, so far as known, of a larger size (about 200 µm). On this basis the specimen is placed tentatively in *Caribachlamys*, and it may well be an early representative of *C. sentis*. The Bowden beds are now considered to be early Pliocene in age (see below, under *Spathochlamys vaginula*).

Secondly, the next oldest fossil *Caribachlamys* thus far discovered occur in the "Pinecrest beds" and Caloosahatchee Formation of Florida of late Pliocene and early Pleistocene age (see below). These specimens, however, are identified with either *Caribachlamys paucirama,* new species, or *C. mildredae,* both of which have morphological features that are more derived than are the corresponding features of *C. sentis* (see preceding discussion of the genus *Caribachlamys* and Fig. 8). This suggests that *C. sentis* itself must have been present before the time of deposition of these beds.

Woodring (1982: 590) identified "*Chlamys sentis* (Reeve)?" from the Emperador Member of the La Boca Formation, Lower Miocene, of Panamá, but neither his illustrated specimen (USNM(P) 647216) nor the other two specimens to which he referred are members of this species. Rather they appear to belong to the genus *Dimarzipecten* Ward, 1992, which is discussed below under *Spathochlamys*, new genus.

Recently Garrafielo and Távora (1989) included *Chlamys sentis* in a list of species from the Pirabas Formation, early Miocene, Brazil. This identification is doubtful, however, because they include *Chlamys japericensis* Ferreira, 1960, originally described from the Pirabas Formation, as a junior synonym of *C. sentis*. A specimen of *C. japericensis* sent to the USNM by Dr. Ferreira has shagreen microsculpture and is not a *Caribachlamys.*

Material examined.—Recent material: USNM: 61 lots containing about 300 specimens, from southern Florida, the Florida Keys, Mexico, Nicaragua, Panamá, and Colombia. MNHN: 4 lots containing 4 specimens, from off Brazil (8° 22.5' S, 12° 56.0 W, and the Abrolhos Archipelago). CAS: 2 lots containing 5 specimens, from Bahía Limón, Panamá and Baía de Todos os Santos, Bahia, Brazil.

Fossil material: USNM: USNM(P) 474635, 1 RV, probably Pleistocene, from the Caloosahatchee River area of south Florida (see preceding discussion).

Caribachlamys ornata (Lamarck, 1819)

(Figs. 6q,r; 7b,e,h,k; 9a,b)

Pecten ornatus Lamarck, 1819: 176, from southern Atlantic Ocean.

Chlamys ornata (Lamarck), Verrill and Bush, 1897: 59.

Types.— Specimens of *Pecten ornatus* in the Lamarck Collection in Geneva are in two lots. One of these, GNH 1088/75, which contains a single pair of matching valves of length 28.2 mm, is selected herein as the lectotype, because the specimen conforms to Lamarck's measurement and is the specimen illustrated by Chenu (1845, pl. 35, figs. 3 and 3a). The second lot, GNH 1088/73, contains five pairs of matching valves some of which clearly belong to species other than *P. ornatus.*

Type locality.— Lamarck's reference to the locality of this species as "l'Océan atlantique austral" is overly generalized. *Caribachlamys ornata* extends south of the Equator for only a short distance to islands offshore from Brazil. The type locality is herein emended to the Antillean region of the western Atlantic,

Diagnosis.— *Caribachlamys* with valves about equal in convexity or with left valve slightly less convex than right but not markedly flattened; closely spaced, fine ribs with early non-scaly phase followed by scaly phase; ribs introduced continuously throughout ontogeny, with more than 70 ribs at distal margin of disk on mature shells; ribs of right valve commonly in clusters of three, those of non-scaly phase of left valve high and I-beam shaped in cross section, with deeply undercut rib flanks; scales fine, closely spaced, erect, distally concave, and open; commarginal lirae well developed in rib interspaces in early ontogeny and fairly uniform in trend and spacing across rib interspaces; antimarginal striae prominent between commarginal lirae and well developed on rib crests.

Morphological variation.— *Caribachlamys ornata,* like its congeners, is of small size, seldom exceeding a height of 40 mm; no geographic trends in maximum size were observed. The degree to which the ribs of *C. ornata* are non-scaly, smooth crested, and I-beam shaped is highly variable both within and among population samples. Furthermore, these features are less well developed on the right valve than on the left valve. Among 30 measured valves from Florida and the Bahamas, the non-scaly phase of ribs in the central sector of the disk was found to disappear at shell heights ranging from 7 to 10 mm on the right valve and from 9 mm to 25 mm on the left valve. There is much less variation in shell color and color pattern than in ribbing. Most *C. ornata* have dark red, maroon, or purple maculations on a light-colored, generally white, background. Distinct orange coloration in this background is relatively rare, occurring in the collections examined from eastern Puerto Rico through the Virgin Islands to Dominica. Specimens from the northern Bahamas, represented by a good suite of specimens in the Delaware Museum of Natural History, are lightly pigmented, and the extent of the I-beam phase of their ribbing is highly variable.

Comparison.— *Caribachlamys ornata* resembles *C. sentis* in both the ribbing-introduction pattern and the microsculpture of the early commarginal stage. *C. ornata* differs, however, from *C. sentis* and all other *Caribachlamys* in having a distinct non-scaly I-beam-shaped ribbing phase in early ontogeny, persisting on the left valve at least to a shell height of 9 mm (refer to preceding section on *C. sentis*).

Living habits.— *Caribachlamys ornata* lives byssally attached beneath rocks and coral heads in shallow water on the more turbulent parts of coral reefs, on hard, rocky bottoms, or in channels with strong currents. The only documented depth records for live specimens are all shallower than 20m. Dead shells, apparently dislodged from reef fronts, have been dredged from as deep as 165 to 180 m (USNM 501824, off Lazaretto, Barbados).

Geographic range.— *Caribachlamys ornata* occurs throughout the Antilles and in the northern Bahamas, southeastern Florida, and the Florida Keys. I have not been able to substantiate its presence in Bermuda, an occurrence which Abbott (1974, p. 443) also questioned. In the south-

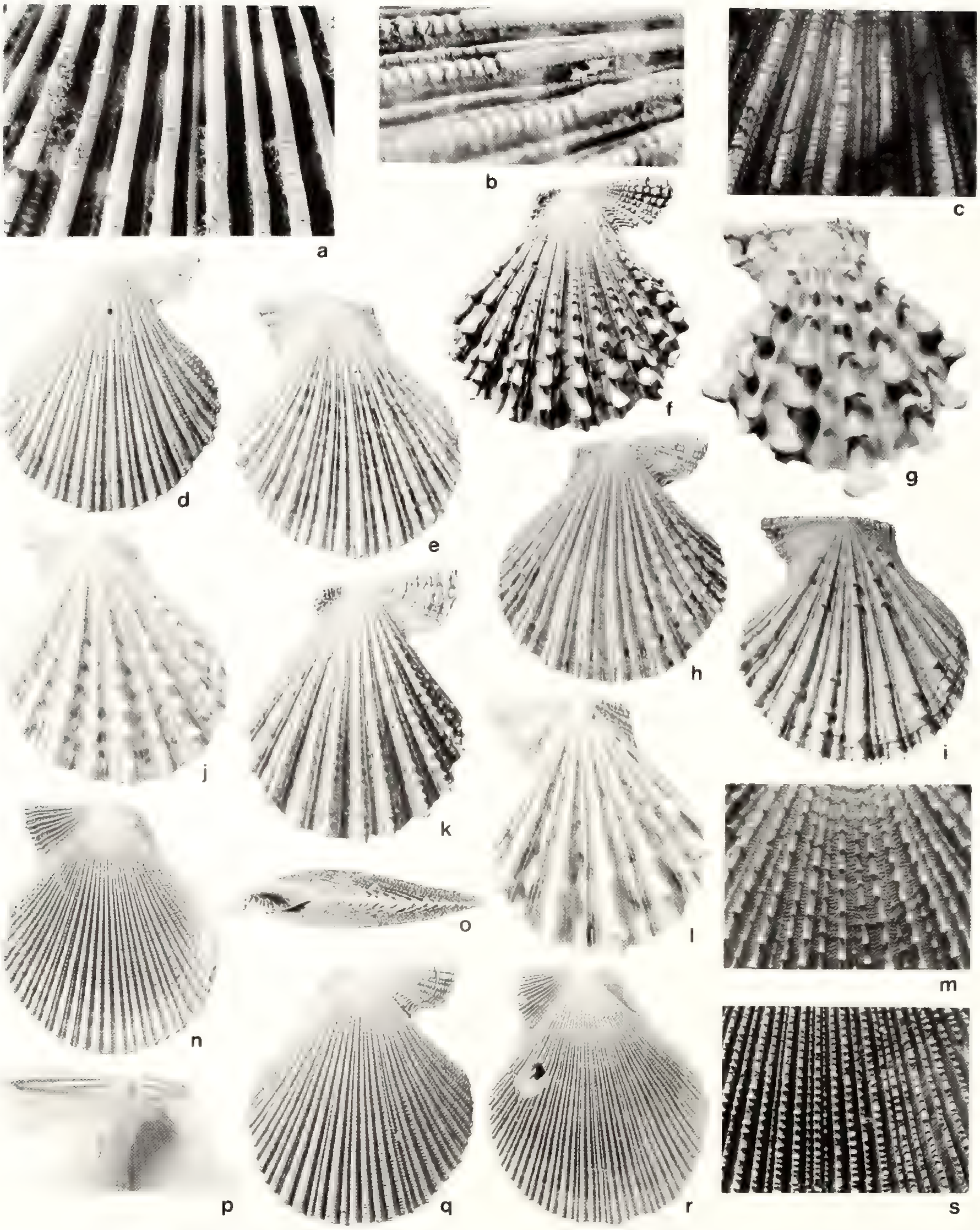

Fig. 9. *Caribachlamys.* **a, b**. *C. ornata*, USNM 683533, The Baths, Gorda Id., Virgin Ids., West Indies, left valve, planar and oblique views of I-beam shaped ribs, horizontal widths of fields 10 mm and 9 mm. **c**. *C. mildredae,* USNM 764745, Long Reef, Florida, juvenile right valve showing irregular commarginal and antimarginal microsculpture in rib interspaces, transmitted light, horizontal field width 4 mm. **d, e**. *C. mildredae,* USNM 598977, holotype, Long Key Reef, Dry Tortugas, Florida, matching right and left valves, height 37.0 mm. **f, g**. *C. imbricata,* USNM 764733, Florida morph, La Chorerra, Havana, Cuba, non-matching right and left valves, heights 29.1 and 25.2 mm. **h, i**. *C. imbricata*, Bermuda morph, USNM 764735, near Bermuda Biological Station, St. Georges, Bermuda, matching right and left valves, height 39.8 mm. **j**. *C. imbricata,* Bermuda morph, USNM 743734, suction dredge spoil from near edge of coral reef, Payardi Id., Minas Bay, Panamá, single left valve, height 30.6 mm. **k, l**. *C. imbricata,* Bermuda morph, USNM 760081, Pico Feo Id., Gulf of San Blas, Panamá, matching right and left valves, height 18.3 mm. **m, o**. *C. paurirama,* UF 24894, Caloosahatchee Fm.?, spoil in Cochran Shell Pit, Hendry Co., Florida, detail of sculpture of left valve, horizontal field width 4.6 mm, and anterior view of articulated shell, shell height 36.5 mm. **n**. *C. paucirama,* USNM(P) 474637, holotype, Caloosahatchee Fm.?, spoil at rock pit east of Ft. Denaud, Hendry Co., Florida, single left valve, height 29.6 mm. **p, q**. *C. paucirama,* UF 24479, Caloosahatchee Fm.?, spoil in Cochran Shell Pit, Hendry Co., Florida, right valve, interior of hinge and exterior, hinge length 15.5 mm, valve height 30.3 mm. **r, s**. *C. paucirama*, USNM(P) 474638, "Pinecrest Beds," northeast of Naples and southwest of Immokalee, Collier Co., Florida, left valve, height 30.7 mm, horizontal field width of detail, 14 mm.

ern and western Caribbean, the species occurs on or near reefs adjacent to islands off Venezuela, Belize, and Quintana Roo, Mexico. In the Gulf of Mexico (other than along the Florida Keys), the species is apparently either very rare or absent. The USNM collections have one poorly documented lot from Veracruz, Mexico (USNM 57655). Rios (1985: 222) reported the presence of this species in the Brazilian islands of Fernando de Noronha and Atol das Rocas.

Stratigraphic range.— Lower? Pleistocene to present.

The oldest fossil occurrences of *Caribachlamys ornata* thus far known are specimens reported by Trechmann (1933: 33) from both high (300 m) and low levels of the Coral Rock of Barbados. Two specimens collected by Trechmann and deposited in The Natural History Museum, London (Palaeontology Section) were examined by me in 1979. Although both clearly belong to *C. ornata,* nothing further can be said about their relationship to modern forms without reexamining the specimens. It was noted at the time that one of the specimens, a left valve from "below the Garrison, west side of Barbados," still retains a remnant of a typical *C. ornata* color pattern. Trechmann (1933) argued that the Coral Rock of Barbados, now tilted and variously displaced by tectonic sliding, may be of fairly uniform age, mainly early Pleistocene. More recent studies (Mesolella, 1967; Ladd *et al.,* 1990) have emphasized that Barbados emerged throughout the Pleistocene.

Specimens of *Caribachlamys ornata* of Pleistocene age have also been collected on San Salvador Island, Bahamas, from a fossil coral reef northwest of the center of Cockburn Town [USNM(P) 474636]. This reef is Sangamonian in age, based on ^{234}U-^{230}Th dates that range from 130.75 ± 1.5 ky to 119.2 ± 1.5 ky (Curran and White, 1989).

Dall (1898) reported that this species occurs in the Pleistocene of the Florida Keys and the Antilles.

Discussion.—There remains some doubt as to whether *Caribachlamys ornata* is distinct from *C. sentis* at the species level or whether the two are merely subspecies. Along the southeastern Florida coast and in the Florida Keys, where both forms occur, there is little doubt that they are well separated morphologically. In the Bahamas, however, particularly at Abaco Island, specimens identified herein as *C. ornata* have only a very short early growth stage with I-beam shaped, non-scaly ribs, and after this phase even shell color can become uniform and similar to that of *C. sentis.* The specimen of Lamarck chosen here as the lectotype in fact is close to these specimens in having a short I-beam phase and an abrupt shift to a more uniform color pattern. A possible interpretation is suggested by the fact that *C. ornata* appears to have a very recent origin in the later Pleistocene. It could well be that the species is still in the process of change and that selection pressures have operated more strongly in reef-front situations in the Lesser Antilles and Florida than on the carbonate banks and patch reefs of the Bahamas.

Material examined.— Recent material: USNM: 93 lots containing about 250 specimens, from the Florida Keys, the Bahamas, Cuba, Grand Cayman, Jamaica, Haiti, the Dominican Republic, Puerto Rico, the Virgin Islands, Saint-Martin, Antigua, Dominica, St. Lucia, Barbados, Tobago, Aruba, Mexico (Quintana Roo), and Belize. DMNH: many specimens from the Bahamas. AM: several lots, from Saint-Martin, St. Eustatius, Barbados, Bonaire, and Curacao.

Fossil material: USNM: USNM(P) 474636, 7 specimens plus fragments from a fossil coral reef northwest of Cockburn Town, San Salvador Island, Bahamas, Pleistocene (Sangamonian, see preceding section on stratigraphic range). BMNH: 2 specimens from the Pleistocene Coral Rock "below the Garrison", west side of Barbados, collected by Trechmann (1933).

Caribachlamys paucirama Waller, new species
(Figs. 9m-s)

Etymology.— From the Latin, *paucus*, meaning few, combined with *ramus,* meaning branch, with reference to the relatively few rib introductions in the late ontogeny of the shell.

Types.— Holotype: USNM(P) 474637, 1 left valve (Fig. 9n), from rock pit at east edge of Ft. Denaud, Hendry County, Florida, probably from the Caloosahatchee Formation of early Pleistocene age. Ht. = 29.6 mm, L. = 25.7 mm, umbonal angle = 92°, AOL = 9.4 mm, POL = 4.3 mm.

Paratypes: USNM(P) 474638 (Figs. 9r,s), 1 left valve, USGS 26543 (TU 1175) from spoil banks along canals south of Florida Highway 858, 3.2km (2 miles) east of junction with Florida Highway 846 (SE$^{1}/_{4}$, section 24, T48S, R27E), northeast of Naples and southwest of Immokalee, Collier Co., Florida. Pinecrest Beds. Collected by S. E. and R. E. Hoerle.

USNM(P) 474639, 1 juvenile right valve and 2 fragments, rock pit 5.6 km (3.5 miles) west of LaBelle, off Florida Highway 78 on north side of Caloosahatchee River, Glades County, Florida. Caloosahatchee Formation.

USNM(P) 474640, 1 right valve, 3 left valves, and 1 fragment, Cochran Shell Pit, NE$^{1}/_{4}$ sec. 23, T43S, R28E, Hendry County, Florida. Collected from spoil, Caloosahatchee Formation.

UF 24479, 1 right valve (Figs. 9p,q) and 2 left valves, same data as preceding.

UF 24894 (Figs. 9m,o), 1 pair of valves, 3 right valves, and 5 left valves, same data as preceding.

UF 24986, 1 left valve, same data as preceding.

UF 41906, 1 right valve, same data as preceding.

UF 55665, 3 right valves and 2 left valves, same data as preceding.

UF 9492, 3 left valves, Caloosahatchee River, Florida, precise locality not specified, presumed to be from the Caloosahatchee Formation.

Diagnosis.— *Caribachlamys* with valves about equally convex; well-spaced, fine, continuously scaly, rounded ribs equal to or narrower than interspaces, with new rib introductions uncommon after mid-ontogeny (shell height of about 15 mm); about 40 to 50 ribs and riblets at margin of mature individuals (shell height of about 30 mm); scales fine, closely spaced, distally concave, and open; commarginal lirae absent; microsculpture in rib interspaces consisting of antimarginal striae of irregular trend in early ontogeny, regularly diverging antimarginal striae in later ontogeny; crests of ribs without antimarginal striae.

Description of holotype.— Exterior: Left valve with height somewhat greater than length (Ht/L = 1.15) and anterior auricle much larger than posterior one (AOL/POL = 2.19); anterior auricle pointed, with deep byssal sinus; posterior auricle oblique, forming an angle with hingeline of about 120°; posterior margin of posterior auricle nearly straight, slightly convex, or slightly concave. Prodissoconch not preserved; radial ribs originating at shell height of 1 mm, initially 10 in number, increasing to 27 at shell height of 5 mm, 37 at 10 mm, and 42 at distal margin at shell height of 30 mm. Ribs high and rounded in cross-section, bearing erect, distally concave, open, closely spaced scales throughout ontogeny; ribs remaining narrower than or equal to interspaces in width. Rib introduction initially mainly by intercalation submedially in interspaces of earlier ribs; microsculpture of pre-radial stage of beak pitted or with short discontinuous antimarginal striae; microsculpture in rib interspaces consisting of striae of irregular, mainly antimarginal, trends; commarginal lirae obscure or absent in early ontogeny.

Interior: Hinge dentition of two-element type as in *Chlamys;* umbonal region aragonitic, without foliated-calcite transgression; adductor and pedal retractor muscle scars not preserved; ribs expressed internally near margin as simple corrugations without internal carinae.

Morphological variation.— The oldest specimen, USNM(P) 474638, from the Pinecrest Beds (Figs. 9r,s), differs from most of the other specimens, all from the Caloosahatchee Formation, in having a slightly greater number of ribs at shell heights of 10 mm and 20 mm, and it exceeds most but not all of the Caloosahatchee specimens in number of ribs present at the distal margin of its disk.

Comparison.— *Caribachlamys paucirama* resembles *C. sentis* in overall aspect but differs in having most of its rib introductions limited to early ontogeny, thereby producing by late ontogeny a far more regular ribbing pattern and a lower total number of ribs at maturity. By the time a shell height of 20 mm is reached, *C. paucirama* rarely has as many as 50 ribs, whereas *C. sentis* has between 50 and 60. Specimens of *C. sentis* that are 30 mm in height or greater have at least 60 radial ribs present along the margins of their disks; in contrast *C. paucirama* generally has fewer than 50. In microsculpture the two species differ in their first 10 mm of growth. Distinct commarginal lirae of fairly regular trend are present in *C. sentis*, whereas *C. paucirama* has irregular antimarginal striae.

Caribachlamys paucirama also resembles *C. mildredae.* The microsculpture pattern of the two species in early ontogeny is very similar but ribbing patterns differ. *C. mildredae* generally has fewer than 30 ribs at a shell height of 10 mm, whereas *C. paucirama* generally has more than 30. The ribs of *C. mildredae* are distinctly clustered on the right valve and distinctly ordered on the left; those of *C. paucirama* tend to be more uniform in spacing and height. Lastly, the scales on the ribs of *C. mildredae*, particularly those on its left valve, are more widely spaced than are the scales of *C. paucirama,* with the scales of some specimens of *C. mildredae* approaching the closed knobby condition that is common in *C. imbricata.*

Paleoecology.— *Caribachlamys paucirama* appears to be most abundant in the Caloosahatchee Formation at sites where there are abundant scleractinian corals. Presumably the living habit and habitat of the new species were similar to, if not the same as, that of extant reef-dwelling members of the genus.

Geographic range.— Thus far known only from southern Florida.

Stratigraphic range.— Middle and Upper Pliocene (Pinecrest Beds) and Lower Pleistocene (Caloosahatchee Formation).

The age of the Pinecrest Beds has been somewhat controversial, depending on how the boundaries for this formation are drawn. The Middle to Late Pliocene age is based on studies by Akers (1974), Waldrop and Wilson (1990: 220), and Jones *et al.* (1991).

Discussion.— *Caribachlamys paucirama* is quite clearly a member of the same clade that contains *C. mildredae* and *C. imbricata,* the shared derived characters being the reduction of early commarginal lirae in rib interspaces, the irregularity of early antimarginal microsculpture, and the reduction in rib number (see preceding section on genus *Caribachlamys* and Figure 8). In its lack of distinct rib clustering, the new species is the most primitive known member of this clade. Although there is only a single specimen of the new species available from the Pinecrest beds, the ribbing pattern of this specimen suggests that between Pinecrest and Caloosahatchee time, rib introductions decreased and rib spacing became more regular. This is just the opposite of a trend that produced *C. mildredae* and *C. imbricata,* in which the ribs are strongly clustered and ordered, with a common trend toward distant spacing of scales on major ribs and toward cusping of scales. This trend in addition to the peculiar microsculpture of *C. paucirama,* with highly irregular antimarginal striae and a lack of commarginal lirae, suggests that the new species is a sister group of a clade that contains both *C. mildredae* and *C. imbricata* (Fig. 8).

Material examined.— USNM: the 10 specimens and fragments listed above as types. UF: the 22 specimens listed above as paratypes.

Caribachlamys mildredae (Bayer, 1941)
(Figs. 9c-e)

Pecten (Chlamys) imbricatus mildredae Bayer, 1941: 46, pl. 3, figs. 16,17.
Pecten (Chlamys) mildredae Bayer, Bayer, 1943: 110, pl. 12, fig. 7.
Chlamys mildredae (F. M. Bayer), Abbott, 1954,: 363, pl. 34, fig. c.

Holotype.—USNM 598977, a pair of matching valves, ht. = 37 mm, from Long Key Reef, Dry Tortugas, depth not specified. Bayer (1941) did not give the locality of the holotype in his original description. In a later note (Bayer, 1942) he specified Biscayne Bay as the type locality on the grounds that the greatest number of shells came from the Miami area.

Diagnosis.— *Caribachlamys* with left valve less convex than right and somewhat flattened; fine, continuously scaly, rounded ribs introduced continuously but sparingly throughout ontogeny, with fewer than 50 ribs and riblets at distal margin of disks of mature individuals; ribs distinctly clustered on right valve and with at least three distinct orders of rib height on left; scales large, widely spaced, commonly strongly inclined distally with tendency to form closed knobs; early commarginal lirae obscure, scarcely higher in relief than intervening antimarginal striae and of irregular trend and spacing; antimarginal striae absent from crests of major ribs.

Morphological variation.— The distinctive and fairly constant feature of *Caribachlamys mildredae* is its ribbing pattern. On the left valve this is commonly expressed as four orders of rib height (Fig. 9e). Ribs of the first order, the highest in amplitude and generally five in number, tend to be more lightly pigmented than the other ribs, which appear to alternate in height between ribs of the next higher order. On the right valve, the ribs tend to be clustered in groups of from two to four (Fig. 9d). As in other species of *Caribachlamys* and *Crassadoma,* the predominant mode of rib introduction is by rib-flank intercalation on the right valve and by either rib-flank or sub-medial intercalation in rib interspaces on the left. Because rib introductions occur throughout ontogeny, the ribs at the margin are of many different sizes. The estimate in the diagnosis that fewer than 50 ribs are produced in mature individuals is based on the largest individuals examined, which have heights between 30 and 40 mm. The major ribs of some individuals have undercut flanks, but because the crests are rounded rather than flattened, the ribs can hardly be called I-beam shaped in cross section. The left valves of all of the specimens examined have a zone in early ontogeny in which the scales atop the major ribs are very widely spaced (spacing between 1.5 and 2 mm). Most specimens have distally open scales, the closed knobby condition being rare.

Coloration of the shell is highly variable, with orange or purple maculations forming in the spaces between major ribs in early ontogeny, the color pattern becoming more uniform later. Some individuals have valve interiors that are yellow, but this is not a constant feature.

Comparison.— *Caribachlamys mildredae* differs from both *C. sentis* and *C. ornata* in having fewer ribs which, on the left valve, are more distinctly ordered. The major ribs of the left valve of some *C. mildredae* have undercut sides but differ from the I-beam shaped ribs of *C. ornata* in lacking flattened, non-scaly, antimarginally striate crests. *C. mildredae* more closely resembles *C. imbricata* in color, including the yellow internal hue, but differs in having four orders of rib height on its left valve and from 40 to nearly 50 ribs and riblets at the distal margin of mature individuals. *C. imbricata,* in contrast, has only three orders or rib height, and its major ribs bear fewer and much larger scales than do those of *C. mildredae.* For a comparison with *C. paucirama,* see the preceding section.

Living habits.— *Caribachlamys mildredae* lives in shallow water (1-20 m) on coral reefs and in crevices on rock jetties, its living habit thus overlapping that of *C. sentis.*

Geographic range.— Thus far *Caribachlamys mildredae* is known with certainty only from southeastern Florida (West Palm Beach southward through Florida Keys to Dry Tortugas). Reports of its presence in Bermuda (Abbott, 1974: 443) are possibly the result of misidentification of what is herein referred to as the Bermuda morph of *C. imbricata* (see below).

Stratigraphic range.— Middle Pliocene? to present.

No unequivocally identified specimens of *Caribachlamys mildredae* are known from the fossil record. There is, however, a small (15.5 mm) left valve from the Pinecrest Beds of Florida that could be an early representative of this species (USNM(P) 474641). It is from the same locality (USGS 26543) that yielded the single Pinecrest specimen of *C. paucirama* in Collier County (see above). This specimen has a greater number of ribs at a shell height of 10 mm than do specimens of extant *C. mildredae* and also a greater number of ribs at its disk margin than would be expected in *C. mildredae* of comparable size. The specimen differs from co-occurring *C. paucirama,* however, in having its ribs distinctly ordered, the largest ribs lacking scales in early ontogeny and later having scales that are much more widely spaced that are those on intervening riblets. The microsculpture of the specimen is consistent with that of either *C. paucirama* or *C. mildredae.*

Discussion.— In his original description of *Pecten (Chlamys) imbricatus mildredae,* Bayer (1941: 46) gave as his basis for linking the new taxon to *P. imbricatus* "the similar scheme of ribbing; the enlarged, sometimes cupped scales; the yellow and purple interior; and the large size of individuals." He did not, however, describe any intergradation between the two taxa, nor did he mention any ecological or geographic separation, both of which would be expected if the two taxa are indeed subspecies. Bayer (1943: 110) later elevated his new "variety" to species rank, while still maintaining that *P. imbricatus* is its closest relative.

Abbott (1974: 443) mentioned that *Chlamys mildredae* "may be a hybrid between *sentis* and *ornata*" but gave no reason why hybridization should not be between *Caribachlamys sentis* and *C. imbricata*, the latter being the species to which Bayer thought *C. mildredae* to be most closely related. At any rate, the hybridization hypothesis seems to have little merit. *C. mildredae* shows no more variation than do associated species; there is no indication of a "hybrid swarm" such as is known to occur commonly in hybridizing situations. It seems more likely, particularly in view of the new species *C. paucirama* described above, that *C. mildredae* is a relict species and that its morphology represents an early stage in the evolution of the *C. imbricata* lineage. This could also explain its present-day rareness and its limited geographic distribution.

Material examined.— Recent material: USNM:11 lots containing 11 specimens; ANSP: 3 lots containing 3 specimens, from southeastern Florida and Florida Keys.

Fossil material: USNM(P) 474641, 1 Right valve, USGS 26543 (TU 1175) from spoil banks along canals south of Florida Highway 858, and 3.2 km [2 miles] east of junction with Florida Highway 846 (SE1/4, section 24, T48S, R27E), northeast of Naples and southwest of Immokalee, Collier Co., Florida. Pinecrest Beds. Collected by S. E. and R. E. Hoerle.

Caribachlamys imbricata (Gmelin, 1791)

(Figs. 7c,f,i,l; 9f-j)

Ostrea imbricata Gmelin, 1791: 3318, living, "in mari rubro" [erroneous].
Pecten imbricatus (Gmelin), Lamarck, 1819: 171.
Chlamys imbricata (Gmelin), Abbott, 1954: 364, pl. 34f.

Type specimens.— The specimen represented by the figure that Gmelin cited, which is in Chemnitz (1784), vol. 7, pl. 69, fig. G, is designated as the lectotype of *Ostrea imbricata* Gmelin. Many of the specimens illustrated by Chemnitz were from the Spengler Collection housed at the Zoological Museum of Copenhagen (Keen, 1966). It is possible that the illustrated specimen of *O. imbricata* could be in that collection. I examined specimens labeled as *Pecten imbricatus* by Lamarck in Paris and Geneva; they all conform to existing concepts of the western Atlantic taxon.

Type locality.— Corrected herein to the Antillean region, western Atlantic.

Diagnosis.— *Caribachlamys* with left valve less convex than right and distinctly flattened; major ribs few in number, commonly 10 on right valve and nine on left, with five ribs on left valve tending to be more prominent and with higher scales than others; secondary riblets variably developed, of much lower height than major ribs; major ribs somewhat trigonal in cross section on right valve, rounded on left; scales on major ribs large, widely spaced, distally concave, commonly forming closed knobs; early commarginal lirae obscured by stronger antimarginal striae and of highly irregular trend; antimarginal striae absent from crests of major ribs.

Morphological variation.— *Caribachlamys imbricata* displays substantial geographic variation, but on the basis of the collections examined this variation appears to be geographically clustered rather than clinal. For purposes of discussion, two intergradational extremes of variation are referred to herein as the Florida morph and the Bermuda morph. Parallel differences between the two are as follows:

Florida morph (Figs. 9f, g): (1) In the early ontogeny of the right valve of the Florida morph, secondary costae that are close to or on the flanks of the primary ribs appear by a shell height of 5 mm. By a height of 10 mm, these secondary costae either disappear or are represented by the expanded, rounded rib flanks of the primary ribs; (2) The posterior auricle of the right valve has unevenly distributed costae, the dorsal one or two closer together and much stronger than the others; (3) On the left valve, third-order riblets are usually absent at least in early ontogeny (up to a shell height of 10 mm) and commonly absent throughout ontogeny; (4) On the left valve, there is usually only one riblet present on the anterior side of the anteriormost primary rib in early ontogeny, increasing to two in later growth. These anteriormost riblets lack scales; (5) On the left valve, radial riblets are unevenly distributed on both auricles, the dorsalmost riblets commonly much stronger than the others.

Bermuda morph (Figs. 9h-l): (1) On the right valve, secondary riblets are distinct and well separated from the primary ones at a shell height of 5mm. At a shell height of 10mm, these secondary costae are still distinct from the major ribs, the major ribs being without expanded flanks; (2) The posterior auricle of the right valve has fairly evenly distributed riblets of even amplitude; (3) On the left valve, third-order riblets are commonly present by a shell height of 10 mm and may be numerous by this stage of ontogeny; (4) On the left valve, there are usually two distinct and fairly strong riblets present on the anterior side of the anteriormost primary rib, commonly increasing to three in later growth. One of these anterior riblets may bear cuspate scales; (5) On the left valve, radial riblets are numerous on both auricles, with only slight or no increase in amplitude toward the dorsal margin.

Caribachlamys imbricata is generally lightly pigmented, the darkest parts being the dark reddish or purple maculations that occur in earlier ontogeny between the primary ribs. Solidly colored shells, such as are common for *C. sentis,* are relatively rare. They have been observed, however, among specimens of the Bermuda morph from the Caribbean coast of Panamá. The valve interiors of both morphs are commonly yellow, sometimes brilliantly so.

Comparison.— *Caribachlamys imbricata* can be distinguished from its congeners by its broad, high-amplitude major ribs. Unlike congeneric species, the scales on these major ribs remain widely spaced throughout ontogeny and commonly form closed knobs.

Living habits.— *Caribachlamys imbricata* lives byssally attached in crevices, beneath coarse rubble and coral heads, and between coral branches on reefs and in both back-reef and fore-reef areas. Depth records for live-collected specimens in museum collections are all shallow, ranging from low subtidal to 20m.

Geographic range.— *Caribachlamys imbricata* appears to have a tropical distribution. It occurs in Bermuda, along the North American mainland only from Miami southward through the Florida Keys, in the Bahamas, and through the Antilles to Curacao and Aruba along the Venezuelan coast. It appears to be absent from the northern Gulf of Mexico, and the only record from the southern Gulf is from Alacran Reef on the north side of the Yucatan Peninsula. Few records are as yet available from the Caribbean coast of Central America with the exception of Belize (offshore cays) and Panamá, which are the best sampled areas. The species is not known from the Atlantic coasts of South America.

All specimens of *Caribachlamys imbricata* from Bermuda examined by me are members of the Bermuda morph, but this morph is also present in Jamaica, Panamá, Colombia, Venezuela, and possibly within samples that also contain the Florida morph in the Bahamas.

Stratigraphic range.— Lower? Pleistocene to present.

The oldest fossils of *Caribachlamys imbricata* thus far found are specimens in the Trechmann collection (BMNH) from the Pleistocene Coral Rock of Barbados at "Cane Garden" and "Highgate". These did not appear in the lists published by Trechmann; the species determinations are based on my examination of the specimens in 1979. As reviewed above in the section on *C. ornata*, Trechmann (1933) considered the Coral Rock to be mainly of early Pleistocene age.

I also found fossil *Caribachlamys imbricata* (USNM(P) 474642) in limestone blocks on Windley Key in the Florida Keys. These blocks presumably came from the Windley Key quarry, which exposes the Key Largo Limestone of late Pleistocene age (Multer, 1969; Stanley, 1966). According to Multer (1969: 109), this limestone represents a back-reef environment and is only about 100,000 years old. Although the specimens are fragmentary, they have ribbing characteristics that suggest that they belong to the Bermuda morph.

The only other known occurrences of fossil *Caribachlamys imbricata*, from Cuba, Haiti, and the

Dominican Republic, also appear to be Pleistocene in age (see below under material examined).

Discussion.— The two extremes of morphology described above as the Florida morph and the Bermuda morph are of considerable interest in that the former is clearly more derived than the latter when they are compared to outgroup taxa within *Caribachlamys*, particularly *C. mildredae*. Among the fossil specimens examined, those from the Windley Key Limestone of Florida (USNM(P) 474642) have ribbing characteristics that suggest that they belong to the Bermuda morph, and this also applies to the specimens from Haiti (USNM(P) 481997 and 481998). The sole Cuban specimen on hand, however, belongs to the Florida morph.

A likely explanation for the extant Bermuda populations, which belong exclusively to the Bermuda morph so far as known, is that they represent dispersal to Bermuda early in the evolution of the species at some time during the Pleistocene. Apparently modern oceanographic conditions do not permit continued dispersal of this species to Bermuda, and most members of populations elsewhere have assumed a more derived condition than those in Bermuda. The presence of Bermuda morphs among some extant populations outside of Bermuda suggests that the Bermuda populations should not be referred to as a geographic subspecies.

Material examined.— Recent material: USNM: 60 lots containing about 150 specimens, from southeastern Florida, Florida Keys, Bermuda, Bahamas, Mexico (Alacran Reef), Jamaica, Cuba, Puerto Rico, Virgin Islands, Anguilla, Barbuda, Curacao, Aruba, Belize, Panamá, Colombia, and Venezuela; MNHN: several specimens from Guadeloupe and 2 specimens in the Lamarck Collection without locality; GNH: 3 specimens in the Lamarck Collection, without locality; AM: specimens from Bonaire, Curacao, and Aruba; UCD, collection of Geerat J. Vermeij: a complete shell of the Bermuda morph from a depth of 5 m in a cave near Runaway Bay, north coast of Jamaica.

Fossil material: USNM: USNM(P) 474642, 7 valves or fragments, Windley Key, Florida, Key Largo Limestone, Upper Pleistocene; USNM(P) 481977 and 481978, 2 LV and 1 RV fragment, USGS 9764, on coast 100 m west of old fort on west side of entrance to Port-de Paix harbor, Departement du Nort Ouest, Haiti, "Bed 2 of section, Pleistocene, collected by W. P. Woodring, 1921; USNM(P) 481998, 1 LV, same locality as preceding; USNM(P) 474810, 1 RV, USGS 7943, Naval Station, Guantánamo Bay, Cuba, 6 to 18 m (20 to 60 ft) above sea level, Pleistocene, collected by P. Bartsch, 1917. BMNH: Barbados, Coral Rock, Pleistocene (see "Stratigraphic Range" for details). FIELD SPECIMENS: Fossils in place in the lowest (and youngest) Pleistocene reef terrace along the south coast of the Dominican Republic east of Boca Chica. (These were too brittle and fragile to remove from the rock.)

Tribe Mimachlamydini, New Tribe

Diagnosis.— Chlamydinae with pitted microsculpture in pre-radial stage of left valve, the pits commonly extending into early radial stage; ribbing pattern simple, with the first ribs introduced in ontogeny tending to remain as major ribs and commonly the only ribs throughout ontogeny; ribs on shell interior usually with carinate edges; commarginal lirae in rib interspaces absent, obscure, or limited to early ontogeny; microsculpture between ribs commonly in a divaricating or herringbone pattern.

Discussion.— The new tribe Mimachlamydini is represented by the extant genera *Mimachlamys* Iredale, 1929, of the eastern Atlantic and Indo-Pacific and *Spathochlamys*, new genus, of the western Atlantic and eastern Pacific. It also includes the extinct genus *Dimarzipecten* Ward, 1992, of the tropical western Atlantic. The tribe forms a bridge between the tribes Crassadomini and Aequipectinini and is a sister group of the Aequipectinini in that both share the common presence of a coarsely pitted left beak before the start of the radial stage and a simple ribbing pattern in which the first ribs introduced tend to remain the major ribs and commonly the only ribs throughout the remainder of ontogeny. In both the Mimachlamydini and Aequipectinini these ribs develop carinate edges on the shell interior. In the Mimachlamydini, however, internal rib carinae are absent in the late ontogeny of the more primitive members of the tribe, whereas in the Aequipectinini these carinae are universally present throughout ontogeny.

Mimachlamydini differ from Aequipectinini in having a plesiomorphic chlamydinid two-element hinge with the resilial teeth not elongated toward the free edges of the auricles. In the Aequipectinini the resilial teeth become larger in size than the dorsal teeth and tend to dominate the hinge structure. Lastly, the Aequipectinini develop characteristic wavy and looped commarginal lirae not present in the Mimachlamydini.

The greatest number of extant species in the Mimachlamydini occurs in the western Indo-Pacific region. The genus *Mimachlamys* in particular contains at least a dozen species but with scores of species-group names available due to the prolific overnaming that characterized typological systematics of earlier days. Among these species are the well known *M. senatoria* (Gmelin, 1791) complex, the colorful *M. nobilis* (Reeve, 1852) of Japanese waters, and the giant *M. townsendi* (G. B. Sowerby III, 1895) of the Red Sea, the last being one of the largest of extant pectinids. In the eastern Atlantic and Mediterranean, the tribe is represented at present only by *M. varia* (Linnaeus, 1758). Phylogenetic relationships of some of these species were recently reviewed by Waller (1991: 31). The tribe is absent in the eastern central Pacific including the Hawaiian Islands, but a pair of extant geminate species assigned herein to *Spathochlamys*, new genus, is present in the tropical American region, one member of the pair in the eastern Pacific, the other in the western Atlantic.

The tribe Mimachlamydini has an extensive fossil record in the Tertiary of Europe beginning in the Paleocene (Waller, 1991: 32) but is poorly represented in the American Tertiary. The new genus *Spathochlamys* is apparently the only member of the group that dispersed through seaway connections from the tropical Atlantic into the eastern Pacific.

Spathochlamys, new genus

Etymology.— Based on the Greek "spathe," meaning spade, in reference to concave-up scales, combined with the genus name *Chlamys,* which in turn is based on the Greek word "chlamys," meaning "mantle".

Diagnosis.— Mimachlamydini with rounded or broadly trigonal ribs separated by interspaces each containing a single very narrow riblet; crests of major ribs bearing narrow erect scales that are concave on their upper (dorsal) sides; edges of ribs on inner surfaces of valves strongly carinate; microsculpture in early rib interspaces obscure or dominated by commarginal lirae which cross interspaces without strong curvature.

Type species.— *Pecten benedicti* Verrill and Bush *in* Verrill, 1897, extant, western Atlantic.

Other Species.— *Pecten vestalis* Reeve, 1853 [= *Pecten (Chlamys)* lowei Hertlein, 1935], extant, eastern Pacific, and *P. vaginulus* Dall, 1898, fossil, Miocene-Pliocene, Caribbean region and southeastern United States.

Geographic range.— Western Atlantic from at least Massachusetts to Brazil and throughout the Gulf of Mexico and Caribbean; eastern Pacific and Gulf of California from southern California to Ecuador and westward to the Galápagos Islands.

Stratigraphic range.— Upper Miocene to present.

Discussion.— The new genus differs in a number of qualitative features from *Mimachlamys*. Both the extant and fossil species of *Spathochlamys* have much more strongly developed carinate edges on the ribs on the inner shell surface than do species of *Mimachlamys*, where these carinae are sometimes minimally developed or restricted to early growth stages (as in *M. varia,* an extant species of the eastern Atlantic). Concave-up scales, which form atop at least some of the ribs in *Spathochlamys*, are unknown among extant species of *Mimachlamys,* where scales are concave-down (i.e. concave side facing toward the ventral margin). Some extinct European middle and upper Tertiary Mimachlamydini, e.g., *M. angelonii* (De Stefani and Pantanelli, 1878), have concave-up scales but lack medial riblets, and other aspects of their morphology suggest that they have a phyletic history that is independent of that of *Spathochlamys.*

There is a strong resemblance in ribbing pattern between *Spathochlamys* and *Dimarzipecten* Ward, 1992, a genus recently introduced to accommodate what its author believed to be a single species, *Pecten crocus* Cooke, 1919, that was originally described from the early Miocene (or late Oligocene) of Anguilla. Ward (1992) stressed that *Dimarzipecten* has a narrow stratigraphic range (restricted to lower Miocene and possibly upper Oligocene) and a broad geographic range extending from the Antilles to the Belgrade, Edisto, and Tampa Formations and correlative stratigraphic units of the Carolinas, Georgia, and Florida. However, I have identified a second apparently undescribed species of *Dimarzipecten* in the Chipola Formation of Florida (USNM(P) 474643 and 474644, from Farley Creek, NE$1/4$ sec. 21, T1N, R9W, Calhoun Co.). This extends the stratigraphic range of the genus into the upper lower Miocene (Burdigalian in age; see Akers, 1972: 10).

Like *Spathochlamys, Dimarzipecten* has a *Chlamys*-like shape, ribs that become trigonal in cross-section at least in late ontogeny, narrow scales atop the ribs, and a fairly regular ribbing pattern with a single medial riblet in each interspace. *Dimarzipecten*, however, differs from Spathochlamys in lacking internal rib carinae and in having convex-up rather than concave-up scales on the rib crests. Furthermore, *Dimarzipecten* has a plesiomorphic microsculptural pattern of coarse antimarginal striae in the rib interspaces. The configuration of these striae is like that present in many modern *Mimachlamys,* including a herringbone-like configuration in rib interspaces in the center of the disk in early ontogeny. In *Spathochlamys*, antimarginal striae are absent or obsolete in early ontogeny except on and near the disk flanks, and commarginal lirae are present in the rib interspaces.

A third genus, possibly new and referred to herein as Genus A pending further research, is characterized by *Pecten sansebastianus* Maury, 1920, of which *P. (Chlamys)* *portoricoensis* Hubbard, 1920, is a junior synonym. This species occurs in the San Sebastian Shale and lower Lares Limestone of Puerto Rico (Maury, 1920; Hubbard, 1920), formations that are considered middle to late Oligocene in age (Maurrasse, 1990, fold-out correlation chart, Column 20). Genus A has a high, narrow shape like that of *Dimarzipecten,* and as in members of that genus, a small medial riblet appears in most rib interspaces in late ontogeny. Like *Spathochlamys,* Genus A has minute concave-up scales on its rib crests and the ribs have strongly carinate edges on the inner surfaces of the valves. Genus A differs from both *Dimarzipecten* and *Spathochlamys* in having a distinctive *Aequipecten*-like microsculpture in rib interspaces in early ontogeny. This pattern consists of wavy commarginal lirae that are strongly looped in a dorsal direction on the rib flanks and in a ventral direction in the rib interspaces; the looped lirae on the rib flanks may become cuspate, as in some *Aequipecten* and in most *Cryptopecten.* Like *Dimarzipecten* and *Spathochlamys*, Genus A lacks a foliated-calcite transgression on the inner surface of its umbonal region, but this is a plesiomorphic state that cannot serve as an indicator of close relationship. Tentatively, Genus A is considered a member of the tribe Aequipectinini based on its microsculptural pattern.

If *Spathochlamys* originated from a species of *Dimarzipecten*, then it seems likely that this origin was within the middle Miocene. The latest *Dimarzipecten* thus far uncovered is the Chipola (Burdigalian) species referred to above, and the earliest undoubted *Spathochlamys* are the specimens of *S. vaginula*, late Miocene and early Pliocene, referred to below. Although fossil specimens of *Spathochlamys* are rare, those that have been brought together for this study suggest that *S. vaginula* of the Miocene and early Pliocene gave rise to both of the extant species but at different times. *S. vestalis* of the eastern Pacific probably originated in the late Miocene; *S. benedicti* of the western Atlantic probably originated in the late Pliocene.

Spathochlamys benedicti (Verrill and Bush, 1897)
(Figs. 10a-k)

Pecten mundus Reeve, 1853, species 151, pl. 33, fig. 151, locality unknown, *non Pecten mundus* M'Coy, 1844, p. 97, Carboniferous of Ireland.

Chlamys benedicti Verrill and Bush, *In:* Verrill, 1897: 74-75, "off Marthas Vineyard, in 1356 fath., dead; West Indies, in 25 to 72 fath., living."

Chlamys benedicti Verrill and Bush, Verrill and Bush, 1898, 20(1139): 834-835, pl. 84, figs. 1-2.

Chlamys verrilli Dollfus, 1898: 180, new name for *Chlamys benedicti* Verrill and Bush, 1897, *non Pecten benedictus* Lamarck, 1819. [invalid new name.]

Pecten (Chlamys) mundus Reeve, Bavay, 1902: 404-406, pl. 8, figs. 8, 9. "European" [erroneous].

Pecten (Chlamys) nympha Bavay, 1906:. 246-247, pl. 7, figs. 3, 4. "Caribæum mare?"

Pecten mundus Reeve, Bavay, 1913: 26, "Bahia" [Brazil].

Chlamys (Chlamys) benedicti Verrill and Bush, Weisbord, 1964: 139-142, pl. 14, figs. 8-11, Playa Grande Formation (Catia Member), "Pliocene" [now dated as Pleistocene], Distrito Federal, Venezuela.

Chlamys (Chlamys) munda Reeve, Fischer-Piette and Testud, 1967: 184-185, Brazil.

Types.— Johnson (1989: 23) designated as lectotype of *Chlamys benedicti* Verrill and Bush a specimen from the Yale Peabody collection (YPM 8833) on the grounds that the "figured holotype" that was supposed to be in the USNM could not be located. The lectotype, a single right valve illustrated by Johnson (1989, pl. 8, fig. 4), is from R/V *Albatross* Stations 2369-2374, 29° 11' 15"N, 85° 29' 32"W, south of Panama City, Florida, 25-27 fm (= 46-49m). In fact, Verrill and Bush (1897) did not specify a holotype in their original description, which referred to specimens from two localities. When they republished the same description a year later, they presented a drawing of one of their specimens, an articulated shell, USNM 202999, from United States Fish Commission [R/V *Albatross*] Stations 2369 to 2374, 25 to 27 fm, Gulf of Mexico between the Mississippi Delta and Cedar Keys, Florida. This is clearly the same set of stations from which the lectotype designated by Johnson (1989) came. Although Johnson's lectotype stands, the specimen illustrated in 1898 (USNM 202999) has now been located in the USNM collections.

The holotype of *Pecten mundus* Reeve, 1853, is a pair of matching valves, the left broken, in The Natural History Museum, London (BMNH 1950.11.14.48). The right valve is refigured herein (Figs. 10a,b).

The holotype of *Pecten (Chlamys) nympha* Bavay, 1906, is the specimen illustrated herein (Figures 10c and 10d). The specimen, which is in Paris (MNHN), is the one that Bavay illustrated and apparently was the only specimen that was available to him at the time that he wrote his description.

Type locality.— Gulf of Mexico, 29° 11' 15"N, 85° 29' 32"W, south of Panama City, Florida, 25-27 fm (= 46-49m).

There is a potential source of confusion regarding the type locality of *Spathochlamys benedicti.* In their original description Verrill and Bush (1897: 75) referred to two

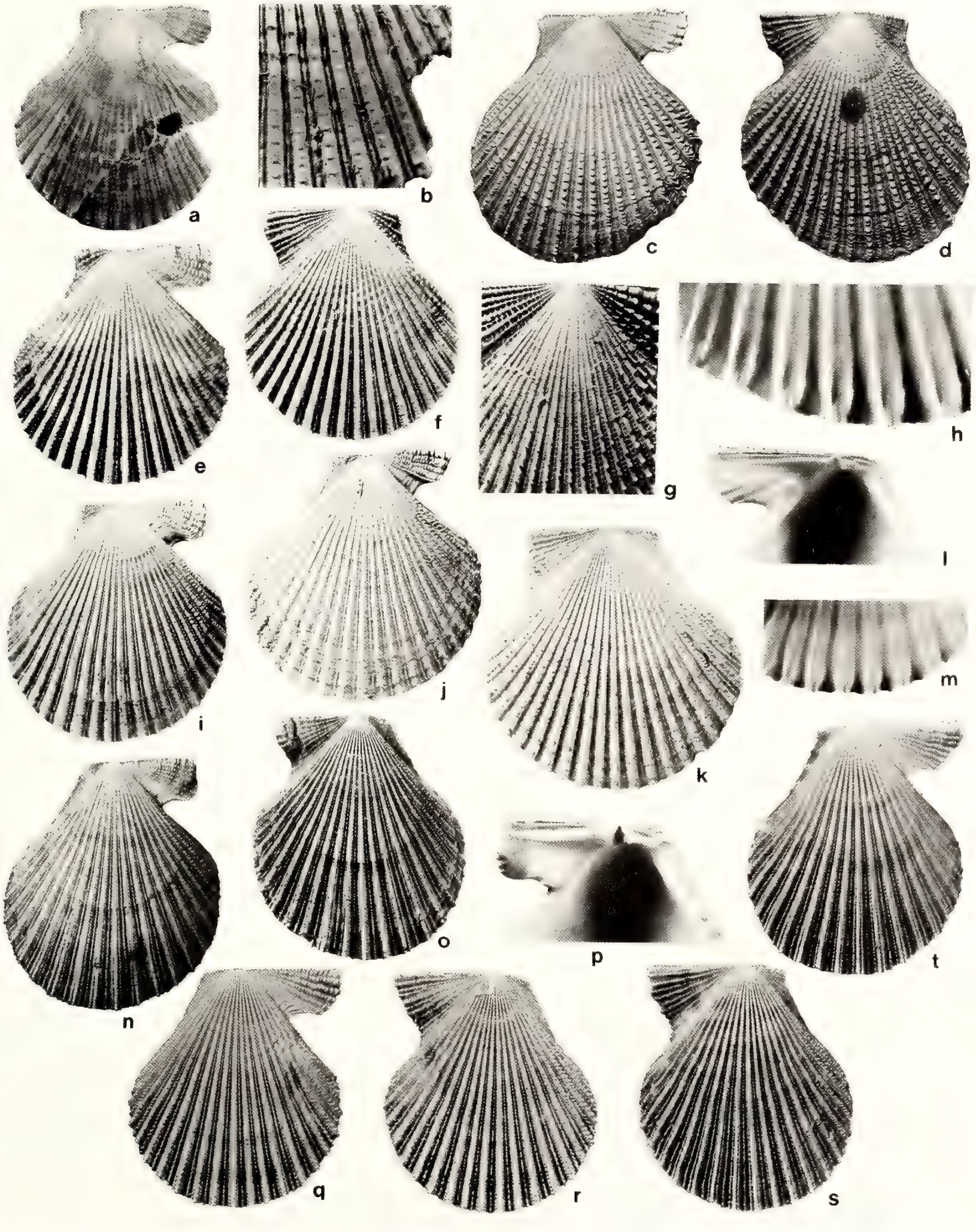

Fig 10. *Spathochlamys*. **a, b**. Holotype of *Pecten mundus* Reeve {= *S. benedicti),* BMNH 1950.11.14.48, locality unknown, right valve uncoated, height 13.3 mm, and detail of surface, horizontal field width 4 mm. **c, d**. Holotype of *P. nympha* Bavay (= *S. benedicti*), Caribbean?, Paris Museum, matching right and left valves, height 15.6mm. **e-g**. *S. benedicti*, USNM 523035, Gulf of Mexico off Carabelle, Florida, matching right and left valves, height 17.0 mm., and detail of left exterior, horizontal field width 5.7 mm. **h**. *S. benedicti*, USNM 764660, Gulf of Mexico off Campeche, Mexico, internal rib carinae of left valve, horizontal field width 9 mm. **i**. *S. benedicti,* USNM(P) 474645, James City Fm., right bank of Neuse River, 3.2 km below James City, Craven Co., North Carolina, right valve, height 21.9 mm. **j**. *S. benedicti*, USNM(P) 474656, Pleistocene?, Minnitimmi Creek, Bocas Island, Panamá right valve, height 17.9 mm. **k**. *S. benedicti*, USNM(P) 474655, Pleistocene?, Bocas Island, Panamá, left valve, height 19.2 mm. **l, m, q, r**. *S. vestalis*, mainland morph, USNM 774188, Gulf of California off Angel de la Guardia Id., Mexico, matching right and left valves: right hinge of length 10.0 mm; internal rib carinae, horizontal field width 9.3 mm; right and left exteriors, valve height 17.8 mm. **n-p**. *S. vestalis* lectotype, BMNH 1992115, "West Indies" [erroneous], matching right and left valves, valve height 22.0 mm, and right hinge of length 9.3 mm. **s, t**. *S. vestalis*, mainland morph, USNM 774191, off North Isle, Pinas Bay, Panamá, matching left and right valves, height 14.9 mm.

localities, one "off Martha's Vineyard, in 1356 fath., dead," the other "West Indies, in 25-*72* fath., living" [italics added]. Specimens from the first locality are present in the Smithsonian collection, catalogued as USNM 52542, USFC Station 2571, with the locality data from that station corresponding to that given in the original description. The lot consists of two right valves, the larger of which is exactly 6mm in height and lemon yellow in color; it is clearly the "largest specimen" referred to by Verrill and Bush in their original description.

In the following year, Verrill and Bush (1898: 834-835, pl. 84, figs. 1, 2) repeated their original description, but this time they provided a drawing of a pair of matching juvenile valves (USNM 202999). Because the description is identical to the first one, it can be inferred that the two localities to which they refer in the second description are also the same as in the first. The deeper station, USFC Sta. 2571, is certainly the same, but the second, from which the illustrated specimen came, presents a problem. In the 1898 description the second locality is given as "stations 2369 to 2374, in 25 to *27* fm [italics added]," and this time no mention was made of the West Indies. The station-book entries for USFC Stations 2369 through 2374 verify the depth range of 25 to 27 fm and give the locality as the Gulf of Mexico between the Mississippi Delta and Cedar Keys, Florida, 1885.

Because there is no material in the Smithsonian collections of *Chlamys benedicti* from the West Indies bearing either the depth range of 25-72 fm as originally published or 25 to 27 fm as published a year later, it is inferred that the references to "West Indies" and "72 fathoms" in the original description were errors and that the specimen later illustrated by Verrill and Bush (1898) from the Gulf of Mexico is one that was before them when they wrote the original description.

Diagnosis.— *Spathochlamys* with length of anterior outer ligament less than twice length of posterior outer ligament; major ribs commonly scaly throughout ontogeny; rib-flank costae poorly developed, not becoming scaly until late ontogeny; posterior auricles erect, with posterior auricular margins forming an angle with hinge line of 90° or less.

Morphological variation.— No apparent geographic trends in size, shell shape, or sculpture were detected across the broad geographic range of this species. The largest specimen examined has a shell height of only 23 mm, and most specimens are in the range of 10 to 15 mm.

Comparison.— *Spathochlamys benedicti* closely resembles its eastern Pacific geminate species, *S. vestalis*. Mature shells of the former have relatively larger posterior auricles, the AOL/POL ratio being less than two, whereas in *S. vestalis* this ratio is greater than two. The posterior auricles of *S. benedicti* have an erect appearance, tending to form a right or acute angle with the hinge, whereas those of *S. vestalis* are uniformly obtuse. Lastly, the rib-flank costae of *S. benedicti* are generally not well developed and seldom bear prominent scales; in *S. vestalis* these same costae tend to develop early in ontogeny and form scales that rival those of the major ribs in height.

Spathochlamys benedicti resembles the extinct western Atlantic *S. vaginula* (Dall, 1898) in shape of disk and auricles but differs in having consistently scaly and trigonal ribs throughout ontogeny, even in the central sector of the disk. In *S. vaginula* the ribs lack scales in early ontogeny in the central part of the disk and are commonly rounded rather than trigonal in cross section. Lastly, *S. vaginula* from the Neogene of the Florida Peninsula attains a much larger size (commonly 30 to 35 mm in shell height).

Living Habits.— The species lives in tropical to temperate waters across a broad range of depths, from about 2 to 800 m, but generally seems to be most common on the middle shelf at depths ranging from about 40 to 90 m (Waller, 1973: 47). The deep byssal notch, prominent active ctenolium, adhering byssal threads on mature dried shells, and data taken at the time of collection all indicate that *S. benedicti* is probably byssally attached throughout life. Individuals attach to a great variety of substrates, including coral debris, sponges, and algal mats (Waller, 1973, and unpub. data). Reed and Mikkelsen (1987) referred to *Chlamys benedicti* as being a common member of the community associated with the scleractinian coral *Oculina varicosa* Lesueur, 1830, off eastern Florida.

Geographic Range.— Although dead specimens have been collected as far north as Latitude 40° 9' N, southeast of George's Bank (the locality referred to by Verrill and Bush in their original description), the distribution of this species is primarily from off Cape Hatteras southward throughout the Gulf of Mexico and Caribbean and as far south as Brazil. Rios (1985: 222) reported the species (as *Chlamys munda*) in Brazil from Amapá to Espirito Santo and in the Abrolhos and Trindade Islands. The species is also present in Bermuda (Waller, 1973).

Stratigraphic Range.— Upper? Pliocene to present.

Fossils of *Spathochlamys benedicti* are reported herein for the first time from the James City Formation of North Carolina (Fig. 10i). There is now substantial agreement that the age of this formation is early Pleistocene (Cronin *et al.,* 1984: 40; Ward and Blackwelder, 1987: 114; Miller III, 1989; Cronin, 1990). Weisbord (1964) reported the species from the Playa Grande Formation (Catia Member) of Venezuela. The age of the Playa Grande Formation is generally considered to be early Pleistocene (Bermúdez, 1980: 303), not early Pliocene as originally stated by Weisbord (1964), but the stratigraphic relationships of formations in the Cabo Blanco area of Venezuela are still controversial (e.g. see, for example, Gibson-Smith, 1976: 4). The fossil occurrences in Costa Rica are from beds now placed in the Moín Formation, which most workers have considered to be Pleistocene in age (e.g. Akers, 1972: 42; Cassell and Sen Gupta, 1989: 147; Robinson, 1990; Lyons, 1991: 159). Coates *et al.* (1992: 821), however, date what are apparently the same beds as late Pliocene-early Pleistocene. The Panamanian fossils (Figs. 10j,k) are all from Bocas del Toro area from beds that contain a fauna that is clearly younger than that of the Miocene Gatun Formation and is assumed herein to be of late Pliocene or early Pleistocene age. Coates *et al.* (1992: 819) have recently described a stratigraphic sequence in this general area that extends in age from the late Miocene through the Pliocene, but they do not specifically mention what is present on Bocas Island and Nancy Cay, the sites that yielded *S. benedicti.* The oldest known representative of *S. benedicti* could be a specimen [USNM(P) 474649] from the Quebradillas Limestone of Puerto Rico. This limestone apparently forms the upper part of the Camuy Formation and may be early Pliocene in age but younger than the Gurabo Formation of the Dominican Republic and the Bowden shell beds of Jamaica (Bermúdez and Sieglie, 1970).

Discussion.— The holotype of P*ecten mundus* Reeve, BMNH 1950.11.14.48, was examined. It is a pair of matching valves, both broken, the right valve (Fig. 10a) having a restored height of 12.7 mm. Reeve's species is clearly a senior synonym of *Chlamys benedicti* but is a junior primary homonym of *P. mundus* M'Coy, 1844, a fossil from the Carboniferous of Ireland.

Dollfus (1898: 180) introduced the new name *Chlamys verrilli* to replace *Chlamys benedicti* Verrill and Bush on the erroneous assumption that Verrill and Bush's name is a junior homonym of P*ecten benedictus* Lamarck, 1819. The endings of the two names, however, differ in case, not in gender, and this is sufficient to prevent homonymy.

Bavay (1902) applied the name P*ecten (Chlamys) mundus* Reeve to two small shells in a collection said to come from Corsica and concluded that the species is "European and even French" [translation]. Although the specimen that he illustrated appears to be what is here called *Spathochlamys benedicti,* there is no reason to believe that the locality data are correct. My own studies of European pectinid collections have not turned up any authentic records of the species in the eastern Atlantic. In a later publication, Bavay (1913: 26) identified shells from Salvador (Bahia), Brazil, as *P. mundus* Reeve, concluding that the species is present on both sides of the Atlantic. In support of this contention, he reported that *P. commutatus* Monterosato, a well-known Mediterranean species, also occurs in Bahia, Brazil. It seems more likely, however, that his *"P. commutatus"* was in fact *Argopecten noronhensis* (Smith, 1885), a species which is known only from the western Atlantic and which may co-occur with *S. benedicti* (Waller, 1973).

Bavay (1906) described *Pecten (Chlamys) nympha* on the basis of a shell in the Paris museum collection. Because the shell was found glued to a board that also held a specimen of *P. antillarum* Récluz, 1853, a well-known Caribbean species, Bavay assumed that his new species also came from that region. The holotype, a pair of matching valves marked by Bavay as the figured type, is refigured herein (Figs. 10c, d). It is clearly a junior synonym of *Spathochlamys benedicti.*

Weisbord (1964: 139), in his report of fossil *Chlamys benedicti* from the Pleistocene Playa Grande Formation of north central Venezuela, referred (p. 141) to "the type" of *C. benedicti* and to "illustrations of the type" but gave no references. He was apparently assuming that the specimen illustrated by Verrill and Bush (1898) is the holotype, although it was never specified as such.

Fischer-Piette and Testud (1967) applied the name *Chlamys munda* Reeve to specimens from Brazil, apparently drawing support from Bavay's (1913) previous report of its occurrence there. Apparently neither Fischer-Piette and Testud (1967) nor Bavay (1902, 1913) were aware that the name *C. benedicti* was already in use for this same species in the western Atlantic.

Material examined.— Recent material: USNM: about 500 lots, from throughout the geographic range of the species; BMNH: syntypes of Reeve (1853) listed in above synonymy; BRM: 7 lots, from Antilles and South America; LM: 18 lots, mainly from off Guyana; MNHN: 7 lots, from South America.

Fossil material: USNM:

North Carolina

USNM(P) 474645, 1 RV, USGS D273, "Croatan Sand", right bank of Neuse River, 3.2 km [2 miles] below James City, Craven County. Collected by MacNeil and Malde, 1954.

USNM(P) 474646 and 474647, 2 RV, James City Formation, about 0.4 km [$^1/_4$ mile] upstream from Johnson Point and at Johnson Point, right bank of Neuse River, Craven County. Collected by T .R. Waller, 1963.

Mississippi

USNM(P) 474648, 10 RV, 12 LV, USGS 24729, shell bed between Clay Units I and II (Morgan *et al.,* 1968, p. 151,152), on Mudlump 90, a mudlump island to the west of the entrance to the South Pass of the Mississippi River delta. Collected by T. R. Waller, 1969.

Puerto Rico

USNM(P) 474649, 1 RV, USGS 19814, Quebradillas Limestone, from sink on Ramey Air Force Base, 1 km west and 3.3 km south of edges of quadrangle, Aquadilla Quadrangle. Collected by C. W. Cooke and A. D. Watt, 1955.

Costa Rica

USNM(P) 474650, 1 LV, USGS 5884b, section exposed in railroad cut, from third fossiliferous zone above level of rails, Moín Hill. Collected by D. MacDonald, 1911.

USNM(P) 474651, 1 LV, USGS 18693, "colline en démolition," Limón. Collected by Pittier, 1898 or 1899.

USNM(P) 474652, 1 RV, 1 LV, USGS 21035, hillside cut and spoils dump at new site of buildings of Colegio de Limón in northeastern outskirts of Puerto Limón. Collected by E. Malavassi, A. A. Olsson, and W. P. Woodring, 1958.

USNM(P) 474653, 2 RV, USGS 21036, scraped hillside slope in Barrio Cementario distinct in southern outskirts of Puerto Limón, east of cemetery. Collected by E. Malavassi, A. A. Olsson, and W. P. Woodring, 1958.

Panamá

USNM(P) 474654, 1 LV, USGS 8306, Bocas Island. Collected by A. A. Olsson, 1917.

USNM(P) 474655 (Fig. 10k), USGS 8307, 1 LV, Bocas group, Bocas Island. Collected by A. A. Olsson.

USNM(P) 474656 (Fig. 10j), USGS 8309, 3 RV, 1 LV, Minnitimmi Creek, Bocas Island. Collected by A. A. Olsson.

USNM(P) 474657, 11 RV, 7 LV, USGS 8349, Bocas group, Conch Point member, Bocas Island. Collected by A. A. Olsson and Sears, 1919.

USNM(P) 474658, 2 RV, USGS 8494, "*Spondylus* group" [apparently with reference to a group of strata], Nancy Cay. Collected by A. A. Olsson, 1919.

Spathochlamys vestalis (Reeve, 1853)

(Figs. 10 l-r; 11 a,b)

Pecten vestalis Reeve, 1853, species 154, pl. 33, fig. 154, "West Indies" [erroneous].

Pecten (Chlamys) lowei Hertlein, 1935: 308-311, pl. 19, figs. 1, 2, 7, 8. "Gulf of California; Galápagos Islands. ?Catalina Island, California."

Types.— The syntypes of *Pecten vestalis* Reeve comprise three specimens: a pair of matching valves and two smaller specimens, one a right valve and the other a non-matching left valve. The first, BMNH 1992115 (Figs. 10n,p), ht. = 22.0 mm, L = 19.3 mm, is the specimen figured by Reeve (1853, pl. 33, species 154) and is selected herein as the lectotype.

The holotype of *Pecten (Chlamys) lowei* Hertlein is a pair of matching valves, California Academy of Sciences, no. 6878, from Carmen Island, Gulf of California, depth 37 m (20 fm) (Hertlein, 1935: 308, pl. 19, figs. 1,2,7,8).

Type locality.— Eastern Pacific off Baja California, Mexico.

Diagnosis.— *Spathochlamys* with length of anterior outer ligament greater than twice length of posterior outer ligament; rib-flank costae beginning on right valve at shell height of less than 12 mm; rib crests with scales ranging from very high in relief to low and sometimes absent on ribs in center of disk; free margin of posterior auricle slightly concave or straight, forming an angle with dorsal margin exceeding 110°.

Morphological variation.— *Spathochlamys vestalis,* like *S. benedicti*, is small in size, seldom attaining a shell height greater than 23 mm. Unlike its western Atlantic counterpart, *S. vestalis* displays some geographic variation in morphology, particularly between mainland populations and those of the Galápagos Islands. These end-points of variation are referred to below as the "mainland morph" and the "Galápagos morph."

The mainland morph (Figs. 10 l-t), which includes the lectotype (Figs. 10n-p), is typified by populations from Santa Catalina Island, California, southward along Baja California, Mexico, throughout the Gulf of California, and along the Mexican coast. These morphs are characterized by the abundant well-developed scales both on the crests of the major ribs and on the secondary rib-flank and medial costae. They also have a conspicuous commarginally lirate stage in early ontogeny. In this early stage, the commarginal lirae are prominent in the rib interspaces and are of higher relief than the proximal ends of the medial costae, which are interrupted by the lirae. The extent of the lirate stage is variable, extending to shell heights from 6 to 10 mm on the right valve and slightly less on the left valve. The number of major ribs is generally 20 or 21, but there may be as few as 17 or as many as 23.

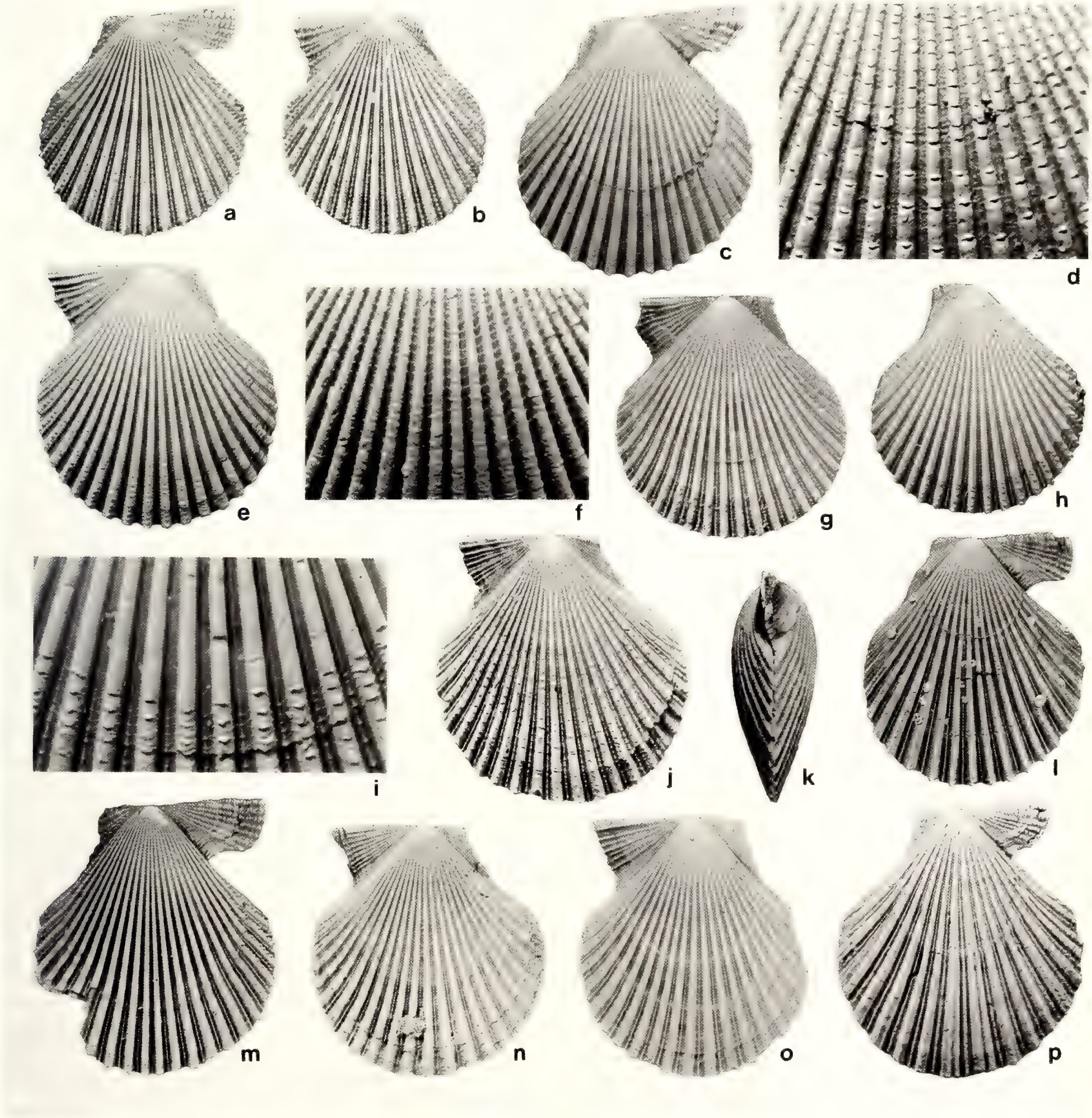

Fig. 11. *Spathochlamys.* **a, b**. *S. vestalis,* Galápagos morph, USNM 774206, Tagus Cove, Albemarle Id., Galápagos Ids., Ecuador, matching right and left valves, height 12.2 mm. **c-f.** *S. vaginula,* lectotype (right valve) and paralectotype (non-matching left valve), USNM(P) 135786, USGS Loc. 2580, Lower Pliocene, Bowden Beds, Bowden, Jamaica: right valve, height 14.4 mm; ribbing of right valve, horizontal field width 5.5 mm; left valve, height 14.5 mm; ribbing of left valve, horizontal field width 7 mm. **g-i**. *S. vaginula,* USNM(P) 474659, Upper Miocene or Lower Pliocene, Gurabo Fm., Río Yaque del Norte, Dominican Republic: left valve, height 13.8 mm; non-matching right valve missing anterior ear, height 12.8 mm; detail of ribbing on left valve at start of scaly phase, horizontal field width 6 mm. **j**. *S. vaginula,* USNM(P) 474660, Upper Miocene or Lower Pliocene, Gurabo Fm., Río Gurabo, Dominican Republic, left valve, height 14.8 mm. **k-o**. *S. vaginula,* Tamiami Fm. *sensu* Waldrop and Wilson (1991) [= "Bed 11"], APAC Pit, near Sarasota, Sarasota Co., Florida: k) USNM(P) 474661, anterior view, height 30.2 mm; l) USNM(P) 474662, right valve, height 33.1 mm; m) USNM(P) 474663, right valve, height 22.8 mm; n) USNM(P) 474664, left valve, height 33.9 mm; **o**. USNM(P) 474665, left valve, height 29.1 mm. **p**. *S. vaginula,* USNM(P) 474666, Upper Miocene or Lower Pliocene, near base of Jackson Bluff Fm., Jackson Bluff, Leon Co., Florida, right valve, height 22.2 mm.

On the basis of the few specimens available for study, mainland morphs from off Panamá (Fig. 10s, t) and Colombia and some of those from off Isla Clarión, Islas de Revillagigedo, Mexico, differ from the typical mainland morphs in having smaller scales and smoother rib interspaces in early ontogeny. They tend to lack conspicuous commarginal lirae in the interspaces of the right valve before the start of medial costae, while their left valves retain a commarginally lirate early growth stage. The absence of commarginal lirae is not due to wear, because fine antimarginal microsculpture is still present in the interspaces.

The Galápagos morph (Figs. 11a,b) differs in having a broader umbonal angle (95 to 100°, in contrast to that of the mainland morph, which has an umbonal angle ranging from 85 to 96°). The Galápagos morph is also somewhat more inflated even though it is smaller in size. The most distinctive feature of the Galápagos morph, however, is the diminutive scales present on the rib crests. The rib crests are somewhat flattened while still retaining a narrow central keel bearing the scales. With few exceptions, specimens from the Galápagos Islands are of this morphology. This morph also occurs, however, off Isla Gorgona, Colombia (LACM: AHF 221-34), and off La Plata Island, Ecuador (LACM: AHF 213-34). Both of these islands are near the shelf edge.

These morphs are not separated by a distinct morphological gap. Transitional specimens occur, although rarely, in the Galápagos Islands and also along the Ecuador coast.

Comparison.— *Spathochlamys vestalis* differs from both *S. benedicti* and *S. vaginula* in having a more asymmetric hinge line, with the anterior outer ligament much longer than the posterior one. The AOL/POL ratio in specimens greater than 12 mm in shell height is generally above 2.05 in *S. vestalis* and is commonly in the range of 2.2 to 2.7. In *S. benedicti* the AOL/POL ratio is generally less than 2.0 and commonly in the range of 1.8 to 1.9. The posterior auricles of *S. vestalis* compared to *S. benedicti* are not only smaller relative to the anterior auricles, but they also are more oblique with a straighter, more inclined posterior margin. This difference in posterior auricular obliquity increases with ontogeny. The secondary rib-flank costae, one on each side of each major rib in the central region of the disk, generally appear earlier in *S. vestalis* than in the other species although there is considerable overlap in time of appearance with that in *S. benedicti*. The medial costae on the right valve of *S. vestalis* generally begin later in ontogeny than in *S. benedicti.* In *S. vestalis* these costae seldom originate before a shell height of 3 mm is reached; in *S. benedicti* the origination point is generally at shell heights ranging from 1.5 to 2.5 mm.

Hertlein (1935: 309) compared his new species, *Pecten (Chlamys) lowei* (= *P. vestalis*), to several fossil species. These fossil taxa, however, are not closely related, and most are now known to belong to the tribe Aequipectinini. This is also true for *Chlamys corteziana* Durham, 1950 (see also Moore, 1984:. B22), which Durham (1950, p. 64) thought resembled *C. lowei. C. onzola* Olsson, 1964, thought by Olsson (1964: 35) to be "probably closest to *C. lowei* (Hertlein)", is also not closely related. I examined the holotype of Olsson's species and found that it is more closely related to the extant eastern Pacific *C. incantata* Hertlein, 1972, of the Galápagos Islands. Hertlein (1972) thought that this Galápagos species "bears a general similarity to that of illustrations of *P. (Chlamys) nympha* Bavay", a species that is now known to be a junior synonym of *Spathochlamys benedicti* (see above). Sculptural details of both *C. onzola* and *C. incantata*, however, indicate that these species both belong in *Veprichlamys* Iredale, 1929, an Indo-Pacific genus that can be placed in the tribe Chlamydini on the basis of its pre-radial microsculpture and lack of internal rib carinae.

Living habits.— The total depth range of live *Spathochlamys vestalis*, based on specimen data in the USNM collection, is from 9 to 183 m, with most specimens having been dredged between 40 and 90 m. Grau (1959) and Bernard (1983) listed depths as shallow as one and two meters, but such shallow occurrences do not appear to be common for living specimens. There do not appear to be any significant differences in the depth preferences of the two morphs described above nor among different parts of the geographic range of the species. Bernard (1983) gave the sea-bottom temperature range of the species as 10 to 29°C. Data on substrate preference and living position are few. Grau (1959: 93) concluded that the species occurs on "rocky, sandy or muddy bottoms, associated with algae, kelp, bryozoa, coral, coralline and sponge." The only specimens in the USNM collections with the bottom type indicated as mud were collected as dead valves. Some specimens show nearly total cover by thin encrusting sponge, and the persistent byssal notch suggests persistent byssal attachment.

Geographic range.— From Santa Catalina Island, California (USNM 774180) southward to Isla La Plata, Ecuador (1° 16' S. Lat.; USNM 774194), in Gulf of California as far north as Bahía San Felipe (USNM 774189), and in the Galápagos Islands (Grau, 1959: 92).

Stratigraphic range.— Upper? Miocene to Recent.

The Upper Miocene limit is based on the occurrence of this species in the Imperial Formation of southern California (Powell, 1986, 1988), discussed below.

Discussion.— Reeve gave the locality for this species as "West Indies", but the morphology of the syntypes (Figs. 10n-p) clearly indicates that they belong to the eastern Pacific species *Pecten (Chlamys) lowei* Hertlein, 1935, which thus becomes a junior synonym of *P. vestalis* Reeve, 1853. The features of Reeve's syntypes that are characteristic of the eastern Pacific species are as follows:

(1) The ratio of the length of anterior outer ligament to length of posterior outer ligament (AOL/POL) is 2.56 in the lectotype and 2.41 and 2.46 in the paralectotypes. These ratios are higher than any found in the western Atlantic species (AOL/POL = 1.76 to 2.03 where height is greater than 12 mm, n=6) but are within the normal range of variation of the eastern Pacific species (2.04-2.88 where height is greater than 12 mm, n=9).

(2) The rib-flank costae of the right valves of the syntypes of *Pecten vestalis* begin at heights of 7.5 and 10 mm. This is earlier than the beginning of comparable costae in the western Atlantic species but is consistent with the ontogeny of these costae in the eastern Pacific species.

(3) The numbers of major ribs on the right valves of the syntypes of P*ecten vestalis* are 21 (lectotype) and 19 (both paralectotypes), lower than the number of major ribs present on right valves of the western Atlantic species (22-24).

Provenance data in nineteenth century works such as Reeve's *Conchologia Iconica* are notoriously inaccurate, and I have uncovered other locality inconsistencies in Reeve's work. That shells from the Pacific side of North America were available to Reeve is indicated by the fact that he described two other pectinids from this region, *Pecten arthriticus* [now *Nodipecten arthriticus*; see Smith, 1991a:. 88) and *P. leucophaeus* [=*Argopecten circularis* (Sowerby); Waller, unpub. data]. Both of these species were listed by Reeve as from unknown localities. Vokes (1991) has commented on similar errors.

The only known reports of *Spathochlamys vestalis* from the fossil record are those of Powell (1986, 1988 reported as *Chlamys lowei*) from the Imperial Formation of southern California. As detailed above, fossil taxa considered closely related to *"Chlamys lowei"* by Hertlein (1935, 1972) and Olsson (1964) are neither ancestral nor congeneric. Moore (1984) listed no records of *S. lowei* in her compendium of Tertiary Pectinidae of California and Baja California, and my own search of the extensive Pacific Coast collections of the USNM did not turn up any specimens. The possibility that this species will eventually be found in strata as old as Pliocene is based on its inferred derivation from an Atlantic ancestor while seaways were still open.

I examined the collection from the Imperial Formation on loan from UCMP to C.L. Powell II at USGS(MP). Two specimens of *Spathochlamys vestalis* were found, both from UCMP Locality A-1415, a part of the section that Powell places in the lower part of the upper member of the formation and interprets as possibly representing a storm deposit formed at inner-shelf depths (Powell, 1993, pers. comm; also see Powell, 1985). One of these specimens is a small incomplete left valve (ht., 9.4 mm) on which rib-flank costae have not yet developed. Medial costae appear to begin late (at about 4.5 mm). These ontogenetic features are consistent with those in *S. vestalis.* The second specimen is a badly crushed and incomplete valve missing its dorsal region. Its original height was probably about 12 mm. Scaly rib-flank costae are present and appear to have formed at a reconstructed shell height of about 7 mm, also consistent with this feature in *S. vestalis.*

The age of the Imperial Formation has been a matter of some debate, but it apparently includes sediments of both Miocene and Pliocene age (Powell, 1985, 1986, 1988; Smith, 1991b). The deposits in the northern Salton Trough area of Riverside County, California, that yielded the specimens of *S. vestalis* appear to be no younger than late Miocene. This age constraint is based on a radiometric (K/Ar) date of about six milltion years obtained from a basalt flow in overlying beds (Powell, 1986, 1988; Smith; 1991b; based on data in Matti *et al.*, 1985).

Material examined.— Recent material: USNM: Pacific Ocean off southern California and Mexico, 7 lots, 22 specimens; Gulf of California, 17 lots, 33 specimens; Panamá, 4 lots, 9 specimens; Colombia, 1 specimen; Ecuador, 1 specimen; Galápagos Islands, 16 lots, about 40 specimens. LACM: Gulf of California, 11 lots, about 50 specimens; Mexico: 7 lots, 10 specimens; Panama: 2 lots, 3 specimens; Colombia: 2 lots, 2 specimens; Ecuador mainland: 3 lots, 4 specimens; Galápagos Islands: 22 lots, 72 specimens.

Fossil material: UCMP Loc. A-1415(RAB 168A): "About the center of the north boundary of NE$1/4$ of NW$1/4$ of section 36, T2S, R3E, [Desert Hot Springs 7.5' Quadrangle, Riverside County, California]. About 1m (50 ft.) south of the divide, in the stream bed of the head of the north directed branch [which separates from the main canyon about 1370 m (4500 ft) from its mouth] of the second canyon east of the Whitewater River. Pebble-bearing siltstone. Collected by R. Bramkamp. (=Burrobend Member)." (Powell, 1986, Appendix 2.) Two valves, both incomplete.

Spathochlamys vaginula (Dall, 1898)
(Figs. 11c-p)

Pecten (Chlamys) ornatus Lamarck? var. *vaginulus* Dall, 1898: 715-716, "Oligocene", Bowden, Jamaica.
Pecten vaginulus Dall, Maury, 1917: 186, pl. 34, fig. 7. Tertiary, Samba Hills, Dominican Republic
Chlamys (Chlamys) vaginulus (Dall), Woodring, 1925:65-66, pl. 8, figs. 1, 2, "Miocene", Bowden, Jamaica.

Types.— Dall (1898: 715-716) mentioned having "seven small valves" of his new variety from the Bowden Beds of Jamaica but provided no illustration, no measurements, and no type designation. This type series was subsequently referred to by Schuchert et al. (1905: 490) as "cotypes" and was catalogued as USNM(P) 135786. The entry for this number in the catalogue, however, mentions only six valves. The discrepancy is apparently due to the recognition, after Dall's 1898 publication, that one of the seven valves does not belong to the same species. (In fact it is an *Argopecten*, not a *Spathochlamys*.) Woodring (1925, pl. 8, figs. 1, 2) provided the first illustrations of members of the type series, a right valve and a non-matching left valve, but continued to refer to these as cotypes. The right valve illustrated by Woodring (1925, pl. 8, fig. 1) is herein selected as the lectotype and refigured (Figs. 11c-f). The type locality is USGS 2580 (see following section on materials examined)

Diagnosis.— *Spathochlamys* with length of anterior outer ligament commonly greater than twice length of posterior outer ligament, especially where shell height exceeds 20 mm; early ribs commonly rounded rather than trigonal in cross section, with scales variably developed or absent; rib-flank costae not appearing until late in ontogeny, generally at shell heights exceeding 12 mm; medial costae variably developed, commonly weak in early ontogeny of left valve; ontogenetic persistence of commarginal lirae in rib interspaces variable, commonly persisting throughout ontogeny, with height of lirae greater than that of medial costae in early ontogeny; posterior margins of posterior auricles slightly concave to nearly straight, forming oblique angle with dorsal margin.

Morphological variation.— In addition to the six valves of the type series from the Bowden Shell Beds of Jamaica, there are about 30 additional valves and fragments from the type locality (USGS 2580) in the USNM collections. The range of variation of these specimens seems to encompass the morphology of specimens from the Gurabo Formation of the Dominican Republic. In general these Bowden and Gurabo specimens have robust simple ribs that tend to be rounded in cross section in early ontogeny, becoming trigonal later. Rib-flank costae are present only on the largest specimens and commonly do not begin to form in ontogeny until a shell height of about 15 mm is reached. The Bowden and Gurabo specimens share rib counts within the range of 21 to 25. Trigonal ribs are common among the specimens from the Dominican Republic but rare among the specimens from Bowden, Jamaica. The Bowden specimens in general have more prominent commarginal lirae in rib interspaces and medial costae that begin later in ontogeny than in the Dominican Republic.

Specimens of *Spathochlamys* from the Tamiami Formation in a pit near Sarasota, Florida (see below), also appear to be within the range of variation of *S. vaginula.* The Tamiami specimens (Figs. 11k-o) differ from those of the Bowden Shell Beds of Jamaica and the Gurabo Formation of the Dominican Republic mainly in being of much greater size, with shell heights ranging from 18 to 34 mm (mean = 27 mm) compared to the maximum shell height of 17 mm for the other samples. Like the Bowden specimens, however, those from the Tamiami Formation have ontogenetically persistent commarginal lirae in rib interspaces, robust rounded major ribs, and late-appearing medial costae.

A single right valve 22 mm in height [USNM(P) 474666, Fig. 11p] was collected by the author from near the base of the Jackson Bluff Formation of Florida (see following discussion of stratigraphy). It resembles the specimens from the Bowden, Gurabo, and Tamiami Formations in having poorly developed scales on the crests of ribs in the center of its disk and in lacking clearly delimited rib-flank costae. The Jackson Bluff specimen differs, however, in having fewer ribs (only 18 at the valve margin compared to 21 to 25 in the other samples). Furthermore, the ribs of the Jackson Bluff specimen are distinctly trigonal in cross-section, and a few of the central ribs bifurcate. The latter feature has been observed to occur in extant species in response to injury or simply as extremes of variation in otherwise simple-ribbed populations.

Comparison.— *Spathochlamys vaginula* differs from both of the extant species, *S. benedicti* and *S. vestalis*, primarily in having less scaly rib crests on the central part of the disk at least in early ontogeny and in having less trigonal ribs at an early growth stage. Many but not all specimens of *S. vaginula* have ontogenetically persistent commarginal lirae in rib interspaces, whereas in the extant species these are limited to early ontogeny.

Weisbord (1964: 142) included both "*Chlamys vaginula* Dall" and "*Pecten (Chlamys) portoricoensis*" in his comparisons for *Spathochlamys benedicti*. As discussed above in the description of *Spathochlamys, P. portori*coensis differs from all *Spathochlamys* species in having an *Aequipecten*-like microsculpture in early ontogeny and is not considered to be congeneric.

Paleoecology.— The molluscan fauna of the Bowden Formation of Jamaica has been interpreted as representing a paleoecological mixture that includes deep-water elements (Woodring, 1928: 37-38). Specimens of *Spathochlamys vaginula* from the Dominican Republic appear to be restricted to facies representing deposition in deeper waters. Saunders *et al.* (1986: 16) noted that depth of deposition increased rapidly in the part of the Gurabo Formation that yielded NMB 15941 and 15835 (see below), with water depths eventually exceeding 200 m. A specimen from about this same level (TU Loc. 1210) is covered by a cemented *Dimya* sp., a genus that is most commonly found at present on the outer continental shelf and slope (H. E. Vokes, 1979: 37). One of the Río Yaque samples, TU 1227A, occurred in a lens interpreted to be a turbidity-flow lens, again suggesting deep water. Scleractinian corals collected at this same locality suggested to Cairns and Wells (1987: 25) a depth of deposition greater than 200 m. The single valve of *S. vaginula* from the Jackson Bluff Formation of Florida (see below) is from the part of this formation determined by DuBar and Taylor (1962: 356) to represent maximum marine transgression and maximum water depth, which they inferred may have been up to 20 fm (37 m) deep. The *S. vaginula*-bearing bed in the pit near Sarasota (Unit 11 of Petuch, 1982a) was interpreted by Petuch (1982a: 19) as representing "a quiet, deeper water lagoonal habitat with depths of around 10 m," but the remains of whales, sharks, and brachiopods suggest to this author that a deeper water environment may have been present. That was also the opinion of E. H. Vokes (1988: 2, footnote), who suggested that the Tamiami deposits in the Sarasota area represent "a more offshore facies" than the overlying Pinecrest Beds.

Geographic range.— North Carolina, Florida, Jamaica, and the Dominican Republic.

Stratigraphic range.— uppermost Miocene (planktic foraminiferal zone N17) through lower Pliocene (upper planktic zone N19/N20).

The definition and age of the Tamiami Formation of south Florida have been matters of considerable confusion, the history of which was most recently summarized by Lyons (1991: 137). In a paper that was written while Lyons's study was in press, Waldrop and Wilson (1990) have further clarified part of this history and have provided some biostratigraphic constraints on the age of the formation in the Sarasota area. They restrict the term Tamiami Formation to beds unconformably underlying the "Pinecrest Beds" in the APAC (or MacAsphalt) Pit at Sarasota. (The latter formational name is preoccupied, and Waldrop and Wilson renamed these beds the Fruitville Formation.) They also report (p. 202) that at some localities near Sarasota the Tamiami Formation interfingers with beds of the upper Bone Valley Formation and that the vertebrate fossils overlying the Tamiami Formation at these sites are of late Hemphillian age. Tedford *et al.* (1987: 183), on the basis of K/Ar and fission-track dates, gave 4.5 to 6 Ma as the age of the late Hemphillian interval (cited incorrectly as 4.5 to 5.0 Ma in Waldrop and Wilson, 1990: 202). This interval thus spans the Miocene-Pliocene boundary, which most workers now agree is at approximately 5 ma (5.2 ma in Haq *et al.*, 1987: 1158). This would suggest that the specimens of *Spathochlamys vaginula* from the Tamiami Formation in the Sarasota area are of either latest Miocene or earliest Pliocene age. The overlying Pinecrest Beds (Fruitville Formation of Waldrop and Wilson, 1990) are apparently middle to late Pliocene in age (Akers, 1972; Waldrop and Wilson, 1990; Jones *et al.*, 1991).

The specimens of *Spathochlamys vaginula* from the Gurabo Formation of the Dominican Republic are probably of approximately the same age as those from the Tamiami Formation at Sarasota, Florida. In the extensive collections from along the Río Gurabo in the Dominican Republic made by Peter Jung and colleagues of the Natural History Museum of Basel, Switzerland, this species occurs in only two samples, NMB 15941 and 15835. These are closely spaced stratigraphically, NMB 15835 occurring only about 2 m above NMB 15941. As stated by Saunders *et al.* (1986: 17), NMB 15941 lies about 5 m below the Miocene-Pliocene boundary if that boundary is demarcated by the first occurrence of the planktic foraminifer *Globorotalia margaritae* Bolli and Bermúdez, 1965. They also note that NMB 15941 represents the approximate stratigraphic position of the nannofossil NN11-NN12 zonal boundary, generally taken to be just below the Miocene-Pliocene boundary. This NN11-NN12 zonal boundary occurs within the upper part of planktic foraminiferal zone N17 (Bybell and Poore, 1991, fig. 2). The only other Río Gurabo specimens known to me are from two localities, USGS 8548 and TU 1210, both of which are apparently close to but somewhat higher than the site of the NMB samples (Saunders *et al.*, 1986, text-figs. 4, 5). Other specimens from the Dominican Republic are from sections along the Río Yaque del Norte, collected by both the U. S. Geological Survey (USGS 8726) and by H. E and E. H. Vokes of Tulane University (TU 1227A).

The Bowden Formation of Jamaica is now generally considered to be within the *Globorotalia margaritae* zone and hence of early Pliocene age (Bolli and Bermúdez, 1965, pp 125, 146; Bolli and Premoli Silva (1973: 479, fig.

2; Jung, 1989: 11). The presence of *G. margaritae* in the Bowden suggests that this formation may be younger than that part of the Gurabo Formation that yielded *Spathochlamys*, which is below the *G. margaritae* zone. In the Dominican Republic the *G. margaritae* zone begins just above the nannofossil NN11/NN12 boundary (upper zone N17) and extends to the NN15/NN16 boundary (Saunders *et al.*, 1986, table 3), this upper limit being near the top of planktic foraminiferal zone N19 (Bybell and Poore, 1991, fig. 2). Both Woodring (1928: 37-38), on the basis of molluscan faunas, and Bold (1971: 327), on the basis of ostracode faunas, considered the Bowden shell beds to be stratigraphically correlative with the Gurabo Formation.

The single, possibly aberrant, valve of *Spathochlamys vaginula* collected from near the base of the Jackson Bluff Formation in western Florida is possibly about the same age as the Gurabo specimens. The lower Jackson Bluff Formation (the Ecphora faunizone) was dated as early Pliocene (middle of Zone N18 to within Zone N19) at its type area at Alum Bluff on the basis of planktic foraminifera, among which is *Globorotalia margaritae* (Akers, 1972: 15 and 20). At Jackson Bluff, from a locality near where the *Spathochlamys* reported here was obtained, Akers (1972: 20) obtained planktic foraminifera that indicated an age ranging from the upper part of Zone N18 to the upper part of Zone N19, but his samples did not include *G. margaritae*. Because the precise location of the foraminiferal samples relative to the base of the Jackson Bluff formation was not specified, it is possible that the *Spathochlamys* collected by me from less than a meter above the base of the formation is near the maximum allowable age (N18) determined by Akers (1972: 15). Zone N18 is just above the Miocene-Pliocene boundary,

Discussion.— *Spathochlamys vaginula* is the closest of the three species of *Spathochlamys* to the probable outgroup genus, *Mimachlamys*, in having the greatest extent of left-valve rib development without scales, the least trigonal rib cross-sections in early ontogeny, the ontogenetically latest appearing medial costae in the rib interspaces, and the most ontogenetically persistent commarginal lirae. The derived features of the eastern Pacific species, *S. vestalis*, relative to the states of characters present in *S. vaginula* include the following: (1) increase in obliquity of the posterior auricle, (2) reduction in the relative size of the posterior ear, and (3) earlier ontogenetic origin of costae on the flanks of the primary ribs, these rib-flank costae becoming more scaly. In *S. benedicti*, two of these characters show opposite trends relative to their condition in *S. vaginula*: (1) The posterior auricle becomes less oblique, its posterior margin forming a 90° or acute angle with the hinge; (2) the posterior auricle increases in relative size. The Gal·pagos specimens of *S. vestalis* appear to be more derived than their mainland counterparts in having a more inflated form, with the rib crests secondarily flattened except for a very low, narrow crest from which very narrow scales develop.

These morphological differences and stratigraphic occurrences imply that *Spathochlamys vaginula* gave rise to both of the extant species but at different times. Speciation seems to have occurred before final seaway closure in the eastern Pacific (based on the occurrence of *S. vestalis* in the Imperial Formation) but after seaway closure in the western Atlantic (based on the earliest known *S. benedicti*).

Material examined.—

Jamaica

USGS 2580. Bowden, Jamaica. Fine sandy stratum in wagon road cut at foot of a hill that is 300 ft high. Collected by J. B. Henderson and C. T. Simpson, 1894. Bowden Shell Beds. Pliocene. 6 valves including the lectotype, catalogued as USNM(P) 135786, and about 30 uncatalogued valves and fragments.

Dominican Republic

NMB 15835. Río Gurabo near highway bridge, Dominican Republic. Gurabo Formation. From macrofossil sample collected by P. Jung, 1978. See Saunders *et al.* (1986, text-fig. 4) for plot of location and stratigraphic position. 4 valves.

NMB 15941. Río Gurabo about 0.6km downstream from highway bridge. Hard massive silt with diverse fauna scattered and in pockets. Gurabo Formation. From microfossil sample collected by J. B. Saunders, 1978. See Saunders *et al.* (1986, text-fig. 4) for plot of location and stratigraphic position. 3 valves.

USNM(P) 474811. USGS 8548. Right bank of Río Gurabo, 500 ft [152 m] below lower ford at Gurabo Adentro Bluff A, Distrito de Monte Cristi, Dominican Republic. Collected by T. W. Vaughan and C. E. Cooke, 1919. 1 valve in several pieces.

USNM(P) 47812. USGS 8726. La Canela, south side of Río Yaque del Norte, 15 km west of Santiago, Dominican Republic. Formation not specified but probably the Gurabo Formation. Collected by T. W. Vaughan, C. W. Cooke, and others, 1919. 1 valve.

USNM(P) 474659 and 474667. TU-1227A. Turbidity-flow lens (about 30 inches [76 cm] long and 6 inches [15 cm] thick) about 2 feet [61 cm] above base of outcrop at point approximately 75 feet [23 m] downstream from highway bridge, Río Yaque del Norte, Dominican Republic. Gurabo Formation. Collected by E. H. and H .E. Vokes. 10 valves (Figs. 11g-i).

USNM(P) 474660. TU-1210. Río Gurabo, east bank, first bluff downstream from bridge on Los Quemados-Sabaneta road (equivalent to USGS 8544, Maury's Zone B), Dominican Republic. Gurabo Formation. [See Saunders *et al.* (1986, text-fig. 5) for plot of locality.] 1 valve (Fig. 11j).

Florida

USNM(P) 474661-474665 and 474813, Macasphalt Co. shell borrow pit complex (currently the APAC Pit) on the eastern outskirts of Sarasota, 0.3 km west of Interstate Highway I-75, sec. 12, T36S, R18E, Bee Ridge Quadrangle, Sarasota Country, Florida. Collection from a drainage ditch and pit floor of the pit that was first opened in December, 1988. Tamiami Formation (*sensu* Waldrop and Wilson, 1990). Collected in July, 1989, and February, 1991 by John Waldrop, Druid Wilson, and Earlene Mitchell. 5 figured specimens (Figs. 11k-o) and 41 not figured.

USNM(P) 474666. Marl pit atop Jackson Bluff on left back of Ochlockonee River a short distance downstream from Lake Talquin Dam, Leon County, Florida. Upper bed of *Ecphora* faunizone 3.5 to 5 feet [0.9-1.5 m] above base of Jackson Bluff Formation. 1 valve (Fig. 11p).

SUMMARY AND CONCLUSIONS

The six species of *"Chlamys"* presently living in the tropical and subtropical western Atlantic (Table 1) are not a monophyletic assemblage, nor are they a single genus, nor are any of them members of the genus *Chlamys* in a strict sense. The only features held in common by these species are their byssate living habit and its attendant form, where the byssal notch is deep, the active ctenolium persistent, and the auricles asymmetric, with the anterior one the larger. The fact that each species is a member of the Caribbean fauna is a coincidence stemming from a variety of circumstances involving very different phylogenetic histories and different times of arrival of ancestral lineages in the western Atlantic.

The different phylogenetic and biogeographic histories of these species are reflected in the fact that their closest extant relatives may be in the western Indo-Pacific, the eastern Atlantic, the western Atlantic, or the eastern Pacific. The morphological study of closely related living and fossil species, coupled with outgroup comparisons based on a continuing study of the Pectinidae on a worldwide basis, has made it possible to construct phylogenies. These phylogenies, coupled with data on present and past distributions, lead to the following conclusions:

1) All six of the extant tropical western Atlantic *"Chlamys"* species have ancestors to the east, in the eastern Atlantic, the Mediterranean, or the western Indo-Pacific. There is no morphological or paleontological basis for supposing that any originated in the eastern Pacific and then dispersed eastward to the western Atlantic.

2) All of the tropical western Atlantic *"Chlamys"* species are constrained by middle latitudes, meaning that it is highly unlikely that they could have dispersed from the western Atlantic to the eastern Pacific by polar routes.

3) The extant tropical American *"Chlamys"* species, as well as the extant eastern Pacific *"Hinnites"*, are distributed among four genera, *Laevichlamys, Crassadoma, Caribachlamys,* and *Spathochlamys*, each of which has a different history of entry into or origin within the Caribbean region. The timing of these origins or arrivals relative to the final closure of the seaways connecting the Caribbean and the eastern Pacific is the primary factor that determines whether geminate species are present in the eastern Pacific. These genus-level histories, which are illustrated diagrammatically in Figures 12-14, are as follows:

Laevichlamys originated in the western Indo-Pacific in the Miocene and dispersed either through the Mediterranean or, more likely, around southern Africa into the eastern Atlantic and thence to the tropical western Atlantic (Fig. 12). The fossil record suggests that its arrival in the tropical western Atlantic and the origin of the Caribbean species *Laevichlamys multisquamata* occurred in post-closure time, i.e. in the late Pliocene or Pleistocene. This is corroborated by the absence of both extant and fossil *Laevichlamys* in the eastern Pacific.

Crassadoma, the type species of which is a cemented form living in the eastern Pacific, has a long and continuous history in the eastern Atlantic, particularly in the Mediterranean (Fig. 13). This history stems from at least the early Miocene, when the Mediterranean was still open at its eastern end to the Indian Ocean. Dispersal to the western Atlantic by members of *Crassadoma* apparently occurred twice (Fig. 13). The first was in the early or middle Miocene, based on evidence that extant *Crassadoma gigantea* of the eastern Pacific is a sister species of *C. multistriata* of the eastern Atlantic. The second entry into the western Atlantic occurred much later, probably in post-closure time, giving rise within the Caribbean to the new genus *Caribachlamys.* The key morphological feature of *Caribachlamys* is its lecithotrophic-type larval shell, possibly an adaptation to sequester larvae in reef habitats that were under stress during the rapid sea-level changes of the Pleistocene. Speciation within *Caribachlamys* has occurred rapidly within the Pleistocene to produce four extant species (*C. sentis, C. ornata, C. mildredae,* and *C. imbricata*) and one extinct Plio-Pleistocene species (*C. paucirama,* new species).

The new genus *Spathochlamys* is represented in

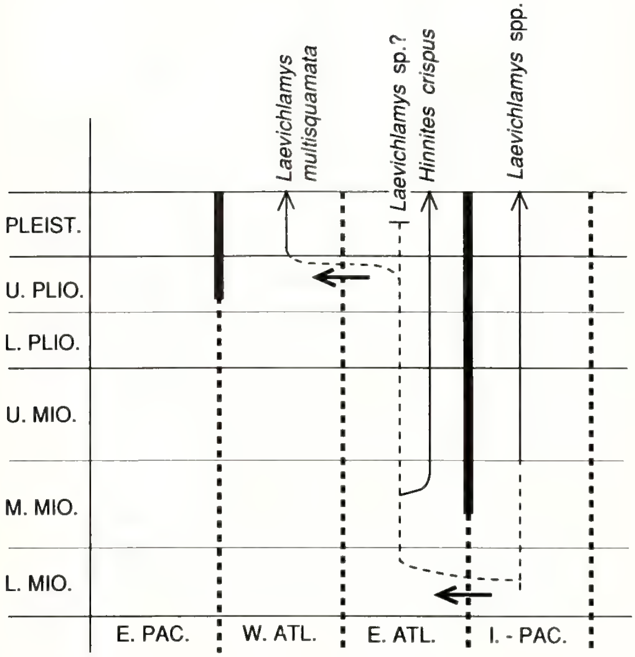
Laevichlamys multisquamata
Laevichlamys sp.?
Hinnites crispus
Laevichlamys spp.
PLEIST.
U. PLIO.
L. PLIO.
U. MIO.
M. MIO.
L. MIO.
E. PAC.
W. ATL.
E. ATL.
I. - PAC.

Fig. 12. The evolution of *Laevichlamys* among world oceans. Solid vertical lines = physical barriers to dispersal; dashed vertical lines = seaways (Tethyan, south African, or central American) or distance barriers; dashed lineage lines = missing data from the fossil record. Arrows indicate dispersal directions based on the polarities of morphological changes and on stratigraphic records.

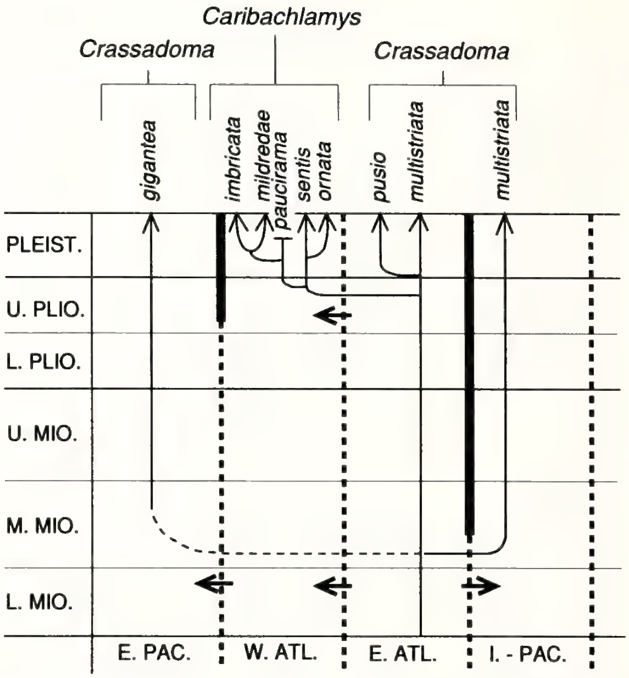
Caribachlamys
Crassadoma
Crassadoma
gigantea
imbricata
mildredae
paucirama
sentis
ornata
pusio
multistriata
multistriata
PLEIST.
U. PLIO.
L. PLIO.
U. MIO.
M. MIO.
L. MIO.
E. PAC.
W. ATL.
E. ATL.
I. - PAC.

Fig. 13. The evolution of *Crassadoma* and *Caribachlamys* among world oceans (symbols are as in figure 5.) *Crassadoma multistriata* is presently distributed around southern Africa into the southwestern Indian Ocean.

the present-day Caribbean by *S. benedicti*, which is the most populous and widespread of all of the extant tropical western Atlantic *"Chlamys"* species. It is also the most eurytopic, living on a variety of bottoms across a span of depths centered on the middle shelf. The genus originated in the tropical western Atlantic in pre-closure time from ancestors in the new tribe Mimachlamydini, which has its most extensive history in the eastern Atlantic and western Indo-Pacific (Fig. 14). The known fossil record of *Spathochlamys* in the western Atlantic is sparse but continuous from the late Miocene, and the succession of morphologies suggests that its entry into the eastern Pacific was in the late Miocene, possibly during a general transgression that permitted deeper water taxa to disperse across seaways that were at other times too shallow. The geminate sister species of *S. benedicti* in the eastern Pacific, *S. vestalis* [=*S. lowei*], at present also has a broad distribution in similar habitats and has dispersed as far westward as the Galápagos Islands with minor morphological divergence from mainland populations.

It is logical to assume that eurytopy bestows resistance to extinction and that stenotopy, coupled with small population size, invites extinction (Stanley, 1986b). The eurytopic species *Spathochlamys benedicti* seems to epito-

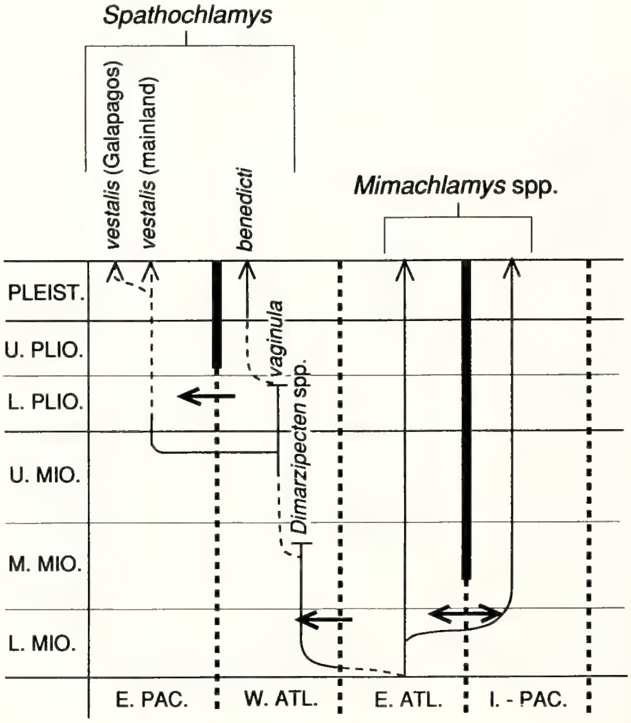
Spathochlamys
vestalis (Galapagos)
vestalis (mainland)
benedicti
Mimachlamys spp.
vaginula
Dimarzipecten spp.
PLEIST.
U. PLIO.
L. PLIO.
U. MIO.
M. MIO.
L. MIO.
E. PAC.
W. ATL.
E. ATL.
I. - PAC.

Fig. 14. The evolution of *Spathochlamys* from *Dimarzipecten* and *Mimachlamys* among world oceans (symbols are as in figure 5).

mize this kind of resistance. It is of interest to note, however, that the lineage of *S. benedicti* has also been resistant to speciation within the western Atlantic in post-closure time. Extant *S. benedicti* is probably a lineage descendant of *S. vaginula*, a species that lived in the tropical western Atlantic during the late Miocene and early Pliocene. The only demonstrable speciation of this lineage is that associated with its dispersal through seaway bottlenecks into the eastern Pacific. Once these seaways were closed, the presumably small founder populations that were isolated in the eastern Pacific were subject either to greater selection pressure or to genetic drift, causing them to diverge from the western Atlantic stem group. The same process is possibly in progress today, forcing divergence of the Galápagos populations of *S. vestalis* that are separated by a deep-water barrier from their mainland counterparts.

Most of the clade originations outlined in the above systematic revision suggest that long-distance dispersal facilitates allopatric speciation. The exception is the endemic Caribbean genus *Caribachlamys,* the most speciose of the three western Atlantic genera. The five species (one extinct) in this genus have apparently all originated since the beginning of the Pliocene within a time span of less than five million years, and one of the species has apparently originated during the Pleistocene. Although the founding populations of this clade may have arrived in the western Atlantic by long distance dispersal from the east, the synapomorphy that unites the species of the genus, and which presumably contributed to its rapid speciation, is a derived prodissoconch morphology (large PI stage and short PII stage) that suggests lecithotrophy and limited dispersal ability.

The key to understanding why a decrease in dispersal ability is associated with rapid speciation in *Caribachlamys* could lie in the common habitat preferences of these species. All are associated with reef-delimited habitats, either reef fronts, reef platforms, or back-reef areas. At present such habitats are not contiguous and are spatially limited; presumably they were even more fragmented during the extensive sea-level fluctuations of the Pleistocene. Reef-adapted byssate pectinid bivalves may have evolved diminished planktic dispersal ability under selective pressure to keep their young in place and to maximize the reproductive potential of local populations. By the same token, if only a very short dispersal phase is present, the possibilities for allopatric speciation are increased by chance transport of these larvae over even relatively short distances. Because all of these species are ctenidial feeders on suspended food particles and do not appear to be gregarious, there is little possibility for direct competition for food. Once reproductive isolation has occurred, daughter species can be reintroduced by chance dispersal into the habitats of their founders. Indeed, the present overlapping geographic ranges of the four extant and to some degree successive species is testimony that this has occurred.

The only strong indication of geographic infraspecific variation within the Caribbean species analyzed here occurs in *Caribachlamys imbricata* from Bermuda. Both outgroup comparison and the fossil record suggest, however, that the Bermuda populations are primitive rather than derived compared to populations from throughout the Antilles and in southeastern Florida. The Bermuda populations are therefore relictual and evidence from the fossil record suggests that gene flow to Bermuda has become restricted beginning in the late Pleistocene.

There has long been a tendency for researchers to view the final closure of the Isthmus of Panamá as an instantaneous event that triggered divergence, speciation, and extinction of once continuous populations of species remaining on the two sides. It is becoming increasingly apparent, however, that the shoaling of seaways was gradual and that divergences occurred both well before and well after closure.

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The zoogeographic implications of the prosobranch gastropods of the Moín Formation of Costa Rica

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Abstract: The deposits of the Moín Formation are located in and around the town of Puerto Limón, on the Caribbean coast of Costa Rica. The fossils date the formation as being Late Pliocene to early Pleistocene in age. The systematics of its constituent prosobranch gastropods were studied, and comparisons made with Recent and fossil gastropod faunas in the Caribbean area. Seventy-one percent of the taxa are living species and for most, this is their first occurrence in the fossil record. These are primarily Caribbean species, but West African/Mediterranean, Panamic and Indo-Pacific elements are also present. Twenty-one percent of the taxa are endemic to these beds, and 8% are typically Mio-Pliocene species occurring for the last time in the fossil record.

A number of species characteristic of the Moín formation have a Holocene distribution in the western Caribbean, extending approximately from the Gulf of Honduras to the northern coast of Colombia, while others have a southern Caribbean distribution, from Costa Rica to across northern South America. These zoogeographic patterns are not well-defined, however, and based on the prosobranch species occurring in the Moín Formation, the existence of specific faunules or other zoogeographic entities in the southwestern Caribbean area cannot be supported.

The deposits of the Moín Formation crop out primarily west and northwest of the town of Puerto Limón on the Caribbean coast of Costa Rica. Historically, the formation has been considered to consist of some 70 m of dark blue claystone to loosely consolidated blue sandy clay with indistinct bedding due to extensive bioturbation, with interbedded lenses of coral reef material. Where bedding is visible, it dips at an angle of 1-2° to the north (Cassell, 1986). With the exposure by bulldozing associated with the urbanization of the peninsula, these beds weather to a reddish-orange clay, with well-preserved fossils eroding out so that they can be easily collected.

Workers in the past have dated the Moín Formation as Miocene or Pliocene in age (Gabb, 1881; Olsson, 1922; Woodring, 1928) using traditional dating methods such as percentages of living species involving Lyellian curves. More recently, using micropaleontological evidence, the Moín Formation has been considered to be early Pleistocene in age (Akers, 1972; Taylor, 1975; Robinson, 1990, 1991) and it has been suggested that the topmost beds extend into the middle Pleistocene (Akers, pers. comm.) or even late Pleistocene (Cassell, 1986). However, Coates *et al.* (1992), have expanded the definition of the Moín Formation, adding another 130 m of underlying sediments, placing most of the formation in the Late Pliocene, with only the topmost strata falling in the Pleistocene. This expanded definition shall remain open to question for the present.

METHODS

Extensive collections of fossil material from the area were made over several years, and the collections made by earlier Tulane University researchers, primarily Drs. Harold and Emily Vokes, were incorporated. The full geographic extent of the Moín Formation is not clearly established, but is believed to underlie most of the tropical forest on the higher elevations of the Limón Peninsula. The collection of fossil material has tended to be opportunistic in nature, being possible only in "windows" of short duration, occurring when briefly exposed by bulldozing of the vegetation preparatory to urban expansion of Puerto Limón. If not immediately built upon, the land is rapidly reclaimed by secondary forest growth within a few months. The molluscs collected from the Moín Formation were compared with taxa from other Caribbean faunas, in particular Mio-Pliocene Gurabo and Cercado Formations of the Dominican Republic, the Pinecrest and Caloosahatchee Formations of Florida, the Agueguexquite Formation of the Isthmus of Tehuantepec, the Limón and Gatún Formations of the Panamic Isthmus, the Cantaure Formation of Venezuela, and the Esmeraldas beds of Ecuador. Of particular importance for comparison were the faunas of the Bowden Formation of Jamaica, the Cabo Blanco Group of Venezuela and the Bermont of Florida, as they are closer in age to the Moín and provide a chronological context for the study. The systematics of all constituent species had to be

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examined with care because of the perspective adopted by the first molluscan systematists working with these various formations. In many cases, the assumption was made that these beds were by and large contemporaneous,and the molluscan taxa contained in one particular formation were therefore common to others. With the increasing accuracy of dating using foraminifera and calcareous nannoplankton indicators, these circum-Caribbean beds are now known to range in age from Miocene to Pleistocene. Many of the molluscan species can now be seen as distinct, as opposed to being regional variants of more widespread taxa, particularly when they can be studied together in a more clearly-defined geographical and chronological context. During this study, collections of comparative Recent shallow-water material were also made from the western Caribbean region, from the Yucatán Peninsula, and the Caribbean coasts of Honduras, Costa Rica (Robinson and Montoya, 1988), and Panamá and Colombia. Deeper water material was collected from the Honduran continental shelf from on board Honduran shrimp boats. Ecological data from living specimens were used to interpret the paleoecological conditions under which the Moín Formation was deposited.

RESULTS

Three hundred and six prosobranch gastropods were identified in this study, and the systematics as well as the paleoecology of these species are currently in preparation. It should be understood that this paper is a preliminary report, with further analysis of the systematics and phylogenetic relationships of the species currently in progress, but some conclusions of interest can already be made.

Effects of the Plio-Pleistocene glaciations

A substantial proportion of the rich Moín fauna (65 species), approximately 21% of the total, appears to be restricted to these beds. The deposition of the portion of the Moín Formation focused on in this study is interpreted here as occurring during a warm interglacial period, which resulted in a short-lived speciation event. While some of these species have already been described (Table 1), a large proportion have not. More collecting needs to be done in the southwestern Caribbean to confirm that all of these species are indeed extinct.

Table 1. Previously described taxa endemic to the Moín Formation.

Calliostoma limonensis Olsson, 1922
Calliostoma castilla Olsson, 1922
Turbo pittieri Dall, 1912
Cochliolepis simplex (Gabb, 1881)
Atlanta ammonitiformis Gabb, 1881
Cerithiopsis limonensis (Gabb, 1881)
Aclis microsculpta Gabb, 1881
Chicoreus prolixus E. Vokes, 1974
Calotrophon ascensus E. Vokes, 1976
Antillophos limonensis (Olsson, 1922)
Cantharus tortuguera Olsson, 1922
Metula limonensis Olsson, 1922
Nassarius caribbeus (Gabb, 1881)
Latirus irazu Olsson, 1922
Agaronia mancinella (Olsson, 1922)
Olivella limonensis Olsson, 1922
Mitra poas Olsson, 1922
Nebularia coralliophila Olsson, 1922
Prunum limonensis (Dall, 1896)
Conus trisculptus Pilsbry and Johnson, 1917
Conus ultimus Pilsbry and Johnson, 1917
Conus limonensis Olsson, 1922
Compsodrillia moenensis (Gabb, 1881)
Cerodrillia limonetta (Olsson, 1922)
Knefastia limonensis (Olsson, 1922)
plus 40 undescribed taxa

Another 8% of the Moín taxa (24 species) represent the last occurrence in the fossil record of a number Mio-Pliocene taxa typical of older fossil beds, including the Bowden, Pinecrest, Cantaure, Gatún and Río Banano Formations (Table 2). Of interest are a number of species that are illustrative of the effects of the initial Plio-Pleistocene glacial pulses. By the time the Moín Formation was deposited, the Caribbean Basin had been subjected to the effects of several glacial episodes, and the composition of the Moín fauna already indicating a significant loss of Mio-Pliocene species, with many groups now considered to be Paciphilic and a number of extinct species characteristic of somewhat older formations, especially the Bowden Formation of Jamaica. It should be noted that although the Bowden is not very much older (considered here as early Late Pliocene) and is geographically close, a substantial portion of its fauna had disappeared by Moín time. Clearly, the differences between the faunas of the Bowden and Moín Formations highlight the effects of one or more of the earlier glacial pulses of the Late Pliocene.

A small but notable constitutent of the Moín fauna is defined by those species extending their geographic ranges or migrating southwards due to climatic deterioration during the Tertiary. Among these are *Trivia* cf. *T. crovae* (Olsson, 1967), *Jenneria* cf. *J. richardsi* Olsson, 1967, and *Niso willcoxiana* Dall, 1889. These species, or

Table 2. Mio-Pliocene species whose last occurrence is in the Moín Formation.

Calliostoma guppyana Gabb, 1881
Turbo saltus Olsson, 1922
Arene lepidota Woodring, 1928
Microstelma cepula (Guppy, 1866)
Modulus basileus Guppy, 1878
Atlanta diamesa Woodring, 1928
Niso willcoxiana Dall, 1889
Cancilla limonensis (Olsson, 1922)
Conus wiedenmayeri Jung, 1965
Conus gracillisimus Guppy, 1866
Conus recognitus Guppy, 1867
Scobinella morieri Laville, 1913
Polystira barretti (Guppy, 1896)
Miraclathurella vittata Woodring, 1928
Glyphostoma moinica Olsson, 1922
Nannodiella amicta (Guppy, 1896)
Saccharoturris consentanea (Guppy, 1986)
Bactrocythara obtusata (Guppy, 1896)
plus 6 undescribed taxa

their immediate ancestors, were characteristic members of the faunas of the Pliocene Pinecrest Formation and were absent from contemporaneous fauas in the Caribbean. Depsite their subsequent occurrence in the Moín Formation, they are absent from contemporaneous Late Pliocene and Pleistocene formations in Florida, indicating a complete displacement of these species by Plio-Pleistocene glacial episodes to the southern Caribbean. Their appearance in the Moín is also their last before complete extinction, resulting from succeeding glacial pulses.

Of particular interest is the *Conus cedonulli* complex, represented in the Moín by *C. ultimus* Pilsbry and Johnson, 1917. The Mio-Pliocene ancestor of this group was *C. consobrinus* G. B. Sowerby I, 1850, that was distributed throughout the Caribbean basin. The species was subsequently restricted southwards to isolated refugia in the southern Caribbean, where it has speciated into a number of sibling species, each with a very limited distribution (Vink and Cosel, 1985). These species live today in a wide arc from the southern Lesser Antilles, along the coast of northern South America and then north to Honduras, although the complex is not as widely distributed as its parent species. Similarily, *C. venezuelanus* Petuch, 1987, a descendent of the widely-distributed Mio-Pliocene *C. planiliratus* G. B. Sowerby I, 1850, survives in a small area in the Golfo de Triste, off northern Venezuela. *C. venezuelanus* evidently had a greater range during Moín time, as it is quite common in the Costa Rica beds.

West African/Mediterranean Influences

Of interest in the Moín Formation also are those faunal elements that are identified with provinces outside of the typical Caribbean. The occurrence of some West African and Mediterranean elements is not entirely unexpected. Ranellids have been shown to have the ability to cross the Atlantic (Scheltema, 1971; Laursen, 1981) and the closely-related bursids appear also to have achieved some level of teleplanic efficiency. *Bufonaria marginata* (Gmelin, 1791) is restricted to the eastern Atlantic and Mediterranean today and throughout its fossil history, except for the occurrence of four individuals (so far) in the Moín Formation. Teleplanic efficiency may be increased by glacially-induced lowered sea temperatures, as suggested by Beu (1970), by delaying larval metamorphosis just long enough to enable an occasional individual to survive the trans-Atlantic crossing. These particular individuals were able to develop into adults here in the southwestern Caribbean, but apparently were never numerous enough to establish a permanent population. Beu (pers. comm.) identified several individuals of *Bursa scrobilator* (Linné, 1758) from the Moín as well. This West African taxon does have a somewhat longer history in the western Atlantic, having been described as *B. mexicana* Perrilliat, 1963, from the Agueguexquite Formation. *B. scrobilator* is now restricted to the eastern Atlantic. Other amphi-Atlantic species occurring in the Moín include *Cerithium guinaicum* Philippi, 1849, *Phalium granulatum* (Born, 1778), *Polinices lacteus* (Guilding, 1843), *Pterotyphis pinnatus* (Broderip, 1833), and *Typhis sowerbii* Broderip, 1833, although there is not enough evidence to determine unequivocally whether these taxa originated in the western or eastern Atlantic.

Connections with the Indo-Pacific

The deep-water barrier between the Indo-West Pacific and the eastern Pacific has only been breached since Late Pliocene (Vermeij, 1978), or perhaps even later, with the migration of some elements of reef-associated faunas. The occasional incursion of teleplanic Indo-Pacific species today into the Panamic province is well-documented (Emerson, 1967 and 1978; Houbrick, 1968; Montoya, 1983), although the establishment of permanent populations of such species is for the most part restricted to offshore island groups, including Cocos, Clipperton and the Galápagos Islands (Hertlein, 1937, 1963; Hertlein and Emerson, 1953; Emerson, 1991). Unfortunately, it is not clear whether species of Indo-Pacific origin crossed into the Caribbean prior to the closure of the last trans-Isthmian seaways. Vermeij (1978) suggested that a warming of the waters around southern Africa during the Pliocene permitted the invasion of marine angiosperm grasses from the Indo-West Pacific. The occurrence of *Smaragdia viridis* (Linné, 1758), *Turbo pittieri* (Dall, 1912) (a turbinid closely related to *T. petholatus* Linné, 1758), *Charonia tritonis variegata* (Lamarck, 1816), *Bursa rhodostoma thomae* (d'Orbigny, 1842) and *Gyrineum louisae* Lewis, 1974 (Robinson, 1990), in the Late Pliocene and early Pleistocene Caribbean Basin supports this possible invasion route; belonging to typically Indo-Pacific supra-specific taxa, they are absent from the eastern Pacific (Panamic) waters and there is no fossil record of their ever having been established in that region.

The first "modern" Caribbean fauna

The Moín fauna represents the first fossil Caribbean fauna that is essentially modern in aspect. Two hundred and seventeen prosobranch gastropod species identified (approximately 71% of the total) are still extant and for the most part, their Moín occurrence represents their first in the fossil record. The environments represented by these species range from the intertidal zones (including mangrove, rock and sand environments), through the various reef zones (lagoonal, back-reef, reef crest and fore-reef environments), with deposition occurring at the base of the fore-reef system at depths of 100 to 200 m. The systematic composition of the fauna has also provided interesting insights into the zoogeography of the region.

It should be made clear that the majority of the living species represented in the Moín fauna are pan-Caribbean in distribution. Smaller numbers of species have a more restricted distribution in the western and/or southern Caribbean, but excessive focus on these particular taxa without keeping in perspective the overall Caribbean nature of the fauna could lead to premature conclusions regarding the subdivision of the Caribbean Province as a whole. The general area is poorly known and for many species, their geographic range is not yet defined. Those Moín species that are living today (or that have a recognizable direct living descendent) and appear to be characteristic of an area extending from the Gulf of Honduras south to Panamá and the adjacent northern Colombian coastline, are listed in Table 3.

Another group of species (Table 4), appear to have a southern Caribbean bias, extending from Costa Rica south to Panamá and east along the northern coast of South Ameica, with some ranging farther south to Surinam and Brazil. It should be noted, however, that some taxa occurring as fossils in Costa Rica, have yet to be found along that coast and are currently known from Colombia or Venezuela and farther east and south, *e.g. Siratus springeri* (Bullis, 1964). Three Moín species that have a southern distribution but occur in two disjunct populations in the southwestern and southeastern Caribbean (not having been reported from the central area), are *Cyclostremiscus schrammi* (P. Fischer, 1857), *Metula lintea* Guppy, 1882 and *Siponochelus tityrus* F. Bayer, 1971.

CONCLUSIONS

The gradual accumulation of both paleontological and neontological systematic and zoogeographic data, of which the current study represents only a fragment, is slowly adding to our understanding of Caribbean zoogeography. The emerging picture is one that is far more complex than that of adjacent provinces. Although the Panamic and Carolinian provinces seem to be relatively homogeneous, with a large proportion of the molluscan species occurring throughout the extent of their respective provinces, the Caribbean appears to be fragmented, with numerous species having quite restricted geographic ranges. The nature of this subdivision, however, remains poorly understood. The implications of this study indicate the possibility of the existence of a western Caribbean and a southern Caribbean fauna. It should be stressed again, however, that the evidence so far does not yet justify the designation of zoogeographic entities on the Subprovince level, particularly in view of the limited numbers of species involved. Just as there are species that apparently define a faunule, there are others whose distribution extend outside the implied boundaries of such a faunule and may even span two such entities, or may change through time. Earlier attempts to subdivide the western Caribbean into subprovinces or faunules (Petuch, 1981, 1990) have been based on small numbers of species. The taxonomic status of a number of newly described taxa used to define these faunas has yet to be fully evaluated and their relationship with closely related taxa is not clearly understood. The Moín taxa and their living descendants do not fit into these subprovincial units and they therefore cannot be used to support these hypothetical constructs. A great deal more work needs to be done in terms of systematics and biogeography of the species (non-molluscan, as well as molluscan) assumed to be endemic to the area before subprovinical boundaries can be defined.

Table 3. Moín species that have a western Caribbean distribution.

Stephopoma myrakeenae Olsson and McGinty, 1958
Cerithioclava garciai Houbrick, 1985
Cerithiopsis caribbaeus (Gabb, 1881)
Haustellum olssoni (E. Vokes, 1967)
*Muricopsis deformis (*Reeve, 1846)
Siphonochelus bullisi Gertman, 1969
Olivella myrmecoon Dall, 1912
Hindsiclava tippetti Petuch, 1987
Voluta virescens Lightfoot, 1786 (including the various named forms)
Agaronia mancinella (Olsson, 1922) (represented by today by *Agaronia hilli* Petuch, 1987 and *A. leonardhilli* Petuch, 1987)
Conus spurius quadratus Röding, 1798
Fusinus gabbi Grabau, 1904

Table 4. Moín species with a southern Caribbean distribution.

Astralium brevispinum (Lamarck, 1822)
Sconsia lindae Petuch, 1987
Siratus springeri (Bullis, 1964)
Murexsul harasewychi Petuch, 1987
Fusinus caboblanquensis Weisbord, 1962
Scaphella evelina F. Bayer, 1971 (represented in the Moín by an undescribed but related species)
Conus baylei Jousseaume, 1872
Conus venezuelensis Petuch, 1987
Hindsiclava cf. *H. chazeliei* (Dautzenberg, 1900)
Persicula interruptolineata (Megerle von Mühlfeld, 1816)

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A database approach to studies of molluscan taxonomy, biogeography and diversity, with examples from western Atlantic marine gastropods

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Abstract: A system of data fields and conventions is introduced that will allow workers on any group of mollusks to build interactive databases documenting classifications, synonymies, geographic and bathymetric ranges, and other summary information at the species level. This system is used to build a database which is the first comprehensive catalogue of Recent Western Atlantic gastropods ever assembled with geographic coverage extending from Greenland to Antarctica. As of January 1993, the database contained 8370 records, of which 3988 represent currently recognized species, 3491 are synonyms, 157 are *nomina dubia* and the remainder are misidentifications, misspellings, invalidly published or extralimital.

There are 3103 currently recognized species of tropical Western Atlantic gastropods (35°N to 24°S); 2641 of these had been named by 1971, when Keen documented 2438 gastropod species in the tropical Eastern Pacific. The common perception that the tropical Western Atlantic fauna is depauperate compared to the Eastern Pacific cannot be supported.

Faunal lists corrected for synonymies, variant generic combinations and misidentifications were extracted from the database for eight areas in the tropical Western Atlantic. These are eastern and western Florida, Yucatan, Panama, Jamaica, Puerto Rico, the Netherlands Antilles and northern Brazil. To correct for regional collecting biases, species smaller than 5 mm, those occurring only deeper than 50 meters, and those lacking external shells were excluded from the lists. In 28 pairwise comparisons among the standardized lists, 27 showed faunal similarities greater than 50%. Western Florida, which lacks shallow reefal habitats, had faunal similarities lower than did eastern Florida, which has these habitats. Habitat availability seems as important as geographic distance in determining faunal similarity within the tropical Western Atlantic. None of the eight regions had more than 4% endemic species. Although species tend to be widespread within the tropical Western Atlantic, only 20% are known from other biogeographic provinces.

Studies of mollusks in the Western Atlantic and throughout the world are hindered by the lack of up-to-date systematic and faunal lists. Researchers attempting to identify or describe species have no comprehensive list of candidate species for comparison. Different names are used for the same species in different regions, making faunal comparisons difficult. Researchers trying to document the effects of extinction, immigration, and speciation on the diversity of various faunas find that reliable estimates of levels of diversity are impossible to obtain even for most shallow-water faunas. Several published catalogues have covered parts of the Western Atlantic fauna in the Northern Hemisphere (Dall, 1889b; Maury, 1922; Johnson, 1934; Abbott, 1974; Turgeon *et al.*, 1988). No catalogue has ever been assembled for the entire Western Atlantic, nor for the tropical Western Atlantic biogeographic province.

Even in such intensively studied areas as the Mediterranean, malacological research has suffered from the lack of comprehensive lists of taxa. Sabelli *et al.* (1990) note the salutary effects of the first modern catalogue of Mediterranean shell-bearing mollusks, that of Piani (1980): a) many researchers adopted the proposed classification thus stabilizing nomenclature; b) the Italian Malacological Society began censusing the Italian marine mollusks, "which would have been inconceivable without a reliable reference list"; c) other researchers were stimulated to produce similar catalogues of Mediterranean opisthobranchs, aplacophorans and cephalopods. Sabelli *et al.* (1990, 1992) themselves recently have finished a 781 page annotated catalogue of Mediterranean mollusks.

The electronic database represents the next step in the production of such catalogues. The potential value of databases in biological research is well-known (Allkin and Bisby, 1984), but this potential has not been realized in malacology. The structure of data fields and conventions introduced here will allow workers on any group of mollusks to build interactive databases documenting classifications, synonymies, geographic and depth ranges, etc. Printed catalogues are static, whereas databases are dynamic. Information in a database can be reorganized (alphabetically, systematically, geographically, chronologically, etc.) to suit the needs of the user. It can be queried in numerous ways, limited only by the ingenuity of the researcher and the types of raw data utilized by the database.

A database must be designed to maximize its ability to answer the questions most likely to be asked of it. A single database that could address the needs of all fields of molluscan research would be extremely complex and cum-

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bersome. The species-level database discussed here has a coarser level of focus than a collection database, summarizing information about the species overall, rather than about particular samples (lots) of a species. Coverage includes all Recent marine gastropod species reported in the Western Atlantic from Greenland to Antarctica.

MATERIALS AND METHODS

More than 1,000 publications on Western Atlantic gastropods were scanned for taxonomic, and bathymetric information. These publications are listed in a bibliographic database linked to the species database. Data come primarily from the published literature, but have also been taken from the malacological collections at the Academy of Natural Sciences of Philadelphia (ANSP) and solicited from researchers expert on the systematics of particular groups. The database contains references to sources of information about each species, to allow verification of the data.

TABLE 1. Data fields used in the database. Numbers give character length of field; N = numeric, A = alphanumeric.

Systematic number	N
Family	A25
Genus	A20
Subgenus	A20
Species	A20
Subspecies	A20
Associated name	A20
Status 1	A1
Status 2	A3
Author	A40
Date	N
Abc	A1
Attributed author	A40
Original genus	A20
Parentheses	A1
Combining genera	A60
Combination	A60
Citation	A20
Figure	A50
Other figure	A50
Type locality	A120
All localities	A150
Ocean	A15
Shell	A1
North	N
South	N
East	N
West	N
Shallow	N
Deep	N
Live shallow	N
Live deep	N
Size	N
Comments	A150
References	A150

For each species-level name applied to a Western Atlantic gastropod, the database attempts to document its status as available, valid, synonymous, dubious, misidentified or misspelled. Note that a species can be valid (i.e. currently recognized), while its currently used name is invalid (e.g. preoccupied). Table 1 lists the fields of information tracked, and the space allocated to them; these fields are described below. Information about geographic, depth and size ranges is entered under the specific name used in a given publication. Geographic, depth, and size data are combined over synonyms to generate summary data for each currently recognized species. If the status of a name is changed from synonymous to valid, or moved from the synonymy of one species to another, its data move with it. The database is thus self-correcting to the degree that the literature provides corrections. Figure 1 shows a subset of database fields and their contents.

The database is currently implemented in Paradox 4.0, but can be easily transported in database or delimited ASCII format to other database programs. It can also be linked to collection databases for comparison of range data and synonymies. The database currently occupies 17 megabytes as a database file, or about 2 megabytes as a delimited ASCII file. A 386 computer or the equivalent is needed for satisfactory performance. [Subsets of the database are available electronically, via Internet from Rosenberg@say.acnatsci.edu.]

DATABASE STRUCTURE AND FORMAT

Data fields, data types and character limits are listed in Table 1; conventions for data entry are described here. Examples of the contents of some fields are shown in Figure 1.

SYSTEMATIC NUMBER: Each family is assigned a number, to allow sorting in systematic order. Alternate classifications can be accommodated by adding fields for numbering schemes that would allow sorting in different orders.

FAMILY: Family names and classification follow Ponder and Warén (1988), Rosenberg (1992) and other recent works.

GENUS: Generic classification follows Turgeon *et al.* (1988), Vaught (1989), and other recent works. Authorities for generic placements are cited in **references.**

SUBGENUS: Conventions are the same as for **genus**. Few data pertaining to subgenera have been entered because there is little agreement on subgeneric classifications and many authors of systematic works do not provide subgeneric placements for the species they treat.

SPECIES: Only the valid or currently recognized specific name of a species is entered here; synonymous names are entered under **associated name**. In cases where species previously synonymized have been recognized as valid by recent workers, citations are given in **references**.

SUBSPECIES: Only the valid or currently recognized subspecific name of a subspecies is entered here; synonymous names are entered under **associated name**. Most subspecies reported in the malacological literature occur sympatrically with the nominate subspecies, because malacological workers until recently treated forms and varieties as subspecies. Subspecies are therefore considered to be synonyms of the nominate form, except in cases where authors have presented evidence for geographical separation of ranges or have raised subspecies to full species.

ASSOCIATED NAME: This field contains all species-group names that have been applied to Western Atlantic mollusks. In the case of currently used specific or subspecific names, the name is repeated here. Synonymous names, misspellings, and misidentifications are entered only here. For *nomina dubia,* the specific name is entered both here and under **species**. If a Western Atlantic species is known from other ocean basins, all known synonyms worldwide are listed.

STATUS 1: Describes the status of a given **associated name:** V = valid (i.e. currently recognized); + = synonym (including misspellings and misidentifications); X = extralimital (for names formerly attributed to the Western Atlantic fauna); D = *nomen dubium* (used to mean "not yet identified" rather than "unidentifiable"). Only one code can be entered for a given name; for synonyms of *nomina dubia,* "D" takes priority over "+."

STATUS 2: Gives additional status information about the **associated name**: ? = questionable synonymy; N = name not available for nomenclatural purposes; S = currently recognized subspecific name; O = objective synonym of the valid name; + = synonym of *nomen dubium.* More than one code can be entered, possible combinations being ?N, ?+, N+, and ?N+.

AUTHOR: The author of a name is here strictly interpreted as the person responsible for a name's being available. Authors of non-binomial, manuscript or nude names later made available are cited under **attributed author**. For misidentifications, "auct. non x" is entered; for misspellings, just "auct." The author responsible for the misidentification or misspelling is entered under **attributed author**. Variant spellings are treated as misspellings unless there is strong evidence that they are intentional, in which case they are treated as emendations. The **author** of a justified emendation is the original author, of an unjustified emendation the emending author. In the case of variant spellings in the original publication, the author's intended spelling is used when this is obvious, with other spellings treated as misspellings.

Constructions such as "x in y" are avoided by citing in the bibliographic database the block of text written by x within y's work. Only in a few cases has this proved impossible, for example, Verrill and Smith in Verrill, where scattered descriptions in Verrill's work are attributed to Verrill and Smith.

DATE: The date of publication is the year in which a name was made available. The exact day and month of publication, if known, and references thereto, are given in the bibliographic database, where the stated date of publication is distinguished from the true date of publication. Misspellings and misidentifications do not have dates of publication in this sense.

ABC: This field distinguishes multiple publications by an author in a single year (e.g. Dall 1889a, 1889b). The species database links to the bibliographic database through the combination of the **author, date**, and **abc** fields.

ATTRIBUTED AUTHOR: Names are often attributed to authors other than those responsible for their publication and availability. Authors of non-binomial, manuscript and nude names later made available are listed here. Other cases include ones such as names being attributed to Lamarck, 1822 by workers unaware that the names were first introduced in Lamarck, 1816. Authors responsible for misspellings and misidentifications are also entered here, not under **author.**

ORIGINAL GENUS: The genus in which the name in **associated name** was placed when first published. Some authors, such as Dall (1889a), often used subgeneric names as if they were generic names, with the generic name placed in a heading. The original genus is taken to be the name that the author stated was the generic name, in accordance with ICZN rules.

PARENTHESES (): If **genus** matches **original genus**, "n" (no) is placed in this field, indicating that no parentheses are needed around author and date when citing the species

Figure 1. Selected fields from the database, showing species of Neritopsidae, Phenacolepadidae, and Pleurotomariidae.

Genus	Species	Subspecies	Status		Associated name	Author	Date	Abc
			1	2				
Neritopsis	*atlantica*		V		atlantica	Sarasúa	1973	
Neritopsis	*atlantica*		+		finlayi	Hoerle	1974	
Phenacolepas	*hamillei*		V		hamillei	Fischer	1857	
Phenacolepas	*hamillei*		+		antillarum	Dall	1889	a
Phenacolepas	*rushii*		V		rushii	Dall	1889	a
Entemnotrochus	*adansonianus*	*adansonianus*	V		adansonianus	Crosse & Fischer	1861	
Entemnotrochus	*adansonianus*	*bermudensis*	V	S	bermudensis	Okutani & Goto	1983	
Perotrochus	*amabilis*		V		amabilis	Bayer	1963	
Perotrochus	*atlanticus*		V		atlanticus	Rios & Matthews	1968	
Perotrochus	*charlestonensis*		V		charlestonensis	Askew	1988	
Perotrochus	*gemma*		V		gemma	Bayer	1965	
Perotrochus	*lucaya*		V		lucaya	Bayer	1965	
Perotrochus	*maureri*		V		maureri	Harasewych & Askew	1993	
Perotrochus	*maureri*		+	N	amabilis	auct. non Bayer	1963	
Perotrochus	*midas*		V		midas	Bayer	1965	
Perotrochus	*notialis*		V		notialis	Leme & Penna	1969	
Perotrochus	*pyramus*		V		pyramus	Bayer	1967	
Perotrochus	*quoyanus*	*quoyanus*	V		quoyanus	Fischer & Bernardi	1856	
Perotrochus	*quoyanus*	*insularis*	V	S	insularis	Okutani & Goto	1985	

name. If they do not match, "y" (yes) indicates that parentheses are needed. This comparison can be automated, except in cases where the original genus was misspelled. For example, if **original genus** is *"Litorina"* and genus is *"Littorina,"* "n" is entered. Other common examples include *"Actaeon"* vs *"Acteon," "Mangilia"* vs *"Mangelia,"* and *"Homalogyra"* vs *"Omalogyra."*

COMBINING GENERA: This field lists genera (and subgenera) with which **associated name** has been combined in the literature.

COMBINATION: Citation of the original combination of names is in the format "Genus (Subgenus) {Section} species status infraspecific-names" along with any notations of uncertainty, such as a genus with a query (?). For "status" the type of name (variety, form, etc.) for infrasubspecific names is indicated. Some authors, such as Dall (1889a) have used sectional in addition to generic and subgeneric names; these are placed in curly braces { }.

CITATION: The pages on which a name is introduced. The entire page range is cited, not just the starting page, to assist interlibrary loan requests. Occurrences of names in indices or tables of contents are not cited unless alternate spellings occur there.

FIGURE: The plate and figure numbers in the original publication. These are separated from **citation** to allow them to be sorted independently, to check, for example, whether all of the figures in a given publication have been cited.

OTHER FIGURE: Illustrations of type specimens not figured in the original publication are cited here. Such illustrations may have been referred to in the original publication (indications), or have been published subsequent to it. Photographs or otherwise improved illustrations of previously figured types are also cited here.

TYPE LOCALITY: It is difficult to eliminate a subjective element in the citation of type localities. Authors frequently give only part of the locality information in the original description, with the rest being contained in the introduction of an article, or an appendix giving station numbers. Country is often omitted entirely by authors who consider it to be obvious. Citations of type localities are therefore paraphrased based on all information available in the original publication, with interpretative comments added in brackets as necessary. In many cases an author lists more than one locality, without explicitly stating a type locality, or mentioning which locality the holotype came from. If an author neglected to state a locality, "not stated" is entered; if an author did not know the locality, "unknown" is entered. Restrictions of type localities by subsequent authors are given in brackets at the end of the field.

ALL LOCALITIES: Abbreviations were assigned to numerous localities at the level of state, province, and island throughout the Western Atlantic (e.g., Lab =

Fig. 1. (continued)

( )	Original genus	North	South	West	East	Shallow	Deep	Shallow live	Deep live	Size
n	*Neritopsis*	23	-20.5	82.5	29.3	0	20			16
n	*Neritopsis*	23	23	82.8	81.3	0	0			17
y	*Acmaea*	28	-28	87	36	0	3			8
y	*Scutellina*	25	25	82	82	0	0			8
y	*Umbraculum*	26	9	80	65	55	55			10
y	*Pleurotomaria*	26.48	13.06	78.67	59.62	107	482	107	366	146
n	*Entemnotrochus*	32.3	32.3	64.8	64.8	366	366			56
y	*Mikadotrochus*	27.73	23	93	80.86	128	411	219	219	80
n	*Perotrochus*	-24	-31	51	45	133	200			72
n	*Perotrochus*	32.73	32.73	78.09	78.09	213	213			87
n	*Perotrochus*	13.2	13.2	59.6	59.6	183	183			47
n	*Perotrochus*	26.48	26.48	78.67	78.67	320	320			32
n	*Perotrochus*	32.73	30.3	80	78.09	193	366	195	213	60
n		32.73	32.73	78.1	78.1	210	198	210	198	45
n	*Perotrochus*	25.93	25.93	78.12	78.12	650	650			118
y	*Mikadotrochus*	-32	-32	51	51	150	150			74
n	*Perotrochus*	16.29	16.29	61.16	61.16	600	600			48
y	*Pleurotomaria*	21.79	12.55	86.4	59.65	128	549	134	350	57
n	*Perotrochus*	32.3	32.3	64.8	64.8	366	366			54

Labrador; Ber = Bermuda; FVen = Falcón, Venezuela). These allow species distributions to be documented more precisely than by **north, south, east**, and **west** described below. Abbreviations are summarized in a separate database table.

OCEAN: Distributions of Western Atlantic species in other oceanic regions are tracked with the following abbreviations: WA = Western Atlantic, EA = Eastern Atlantic, IO = Indian Ocean, WP = Western Pacific, EP = Eastern Pacific, AO = Arctic Ocean, SO = Southern Ocean. Data in **north, south**, and the four **depth** fields are taken only from Western Atlantic records.

SHELL: Four abbreviations (s = shell, i = internal shell, v = vestigial shell, n = no shell) can be used, for example to look at the systematic distribution of shell reduction and loss, or to include only readily fossilizable taxa in comparisons to the fossil record.

NORTH: The farthest north in decimal degrees that the **associated name** has been reported in the Western Atlantic, from the mid-Atlantic ridge westward, including East Greenland, but excluding Iceland.

Latitudes and longitudes are converted to decimal degrees, allowing this and the next three fields to be numeric rather than alphanumeric. Database programs allow mathematical operations on numeric fields but not on alphanumeric ones. Latitudes below the equator are entered as negative numbers, e.g. 23°25'S is entered as -23.42.

SOUTH: The farthest south in decimal degrees that the **associated name** has been reported in the Western Atlantic, including the Antarctic Peninsula, Tierra del Fuego, and Ascension Island, but not St. Helena.

EAST: The farthest east in decimal degrees that the **associated name** has been reported in the Atlantic, limited to a minimum of zero. Longitudes east of Greenwich are not reported.

WEST: The farthest west in decimal degrees that the **associated name** has been reported, to a maximum of 180° for circumtropical or circumpolar species. Longitudes west of 180° are not reported.

SHALLOW: The shallowest depth in meters, with "0" indicating intertidal or beach-collected specimens. Note: in this and the other three depth fields, only "proven" depths are reported. If a species has been reported only in one dredge haul from 100-130 meters, "130" is entered in **shallow** and "100" in **deep**, corresponding to the shallowest and deepest it has been proven to occur. Similarly, if it is known from two dredge hauls, one from 100-130 meters, the other from 170-190, "130" is entered in **shallow** and "170" in **deep**.

DEEP: The deepest recorded depth in meters. Exact conversions are given from feet and fathoms, with the caveat that this can imply accuracy not inherent in the original number (e.g. 100 fathoms = 183 meters).

LIVE SHALLOW: The shallowest depth in meters reported for live-collected specimens, with negative numbers indicating supratidal occurrence.

LIVE DEEP: The deepest depth in meters reported for live-collected specimens.

SIZE: The maximum size, in millimeters, for any dimension.

COMMENTS: Any comments necessary to explain or modify entries in other fields. Preoccupied, replacement, nude, and non-binomial names are noted here. If an author declared a name to be a *nomen oblitum* during the period when that provision of the ICZN was in force, that is noted here.

REFERENCES: Sources of information in the other fields are documented here by citation of author and date followed by a series of codes: D = maximum depth; d = minimum depth; L = maximum live depth; l = minimum live depth; N = north; S = south; E = east; W = west; M = maximum size; C = current classification; + = synonymy; V = valid; T = lectotype or neotype designation or restriction of type locality. Multiple references are separated by semicolons. A typical entry in **references** might look like this: Dall (1889a) DLlW; Abbott (1974) dNM; Leal (1991) SE.

Other fields beyond those noted here are possible, and can be added depending on the needs of a particular researcher. One could record protoconch size and whorl number; references to protoconch, radular and anatomical illustrations; substrate preference; feeding type; reproductive mode; depositories and catalogue numbers of type specimens; and so on, *ad infinitum.*

RESULTS AND DISCUSSION

WESTERN ATLANTIC GASTROPOD DIVERSITY

The database currently contains 8370 records for Western Atlantic marine gastropods from Greenland and Northern Canada through Antarctica. Statistics concerning these records are summarized in Table 2. Of these records, 3988 are for species currently recognized as valid. This means that the species has not been synonymized since it was named, or if it has been synonymized, some author has presented strong arguments that it should be taken out of synonymy.

Currently recognized species somewhat outnumber the 3491 validly published synonyms. The synonymy ratio is 0.88:1, about half the 1.64:1 estimated by Clench (1959) for the Western Atlantic. Boss (1971) has estimated synonymy ratios for mollusks overall to be in the range of 4:1. This ratio would predict 1496 valid species and 5983 synonyms among the 7479 names for Western Atlantic gastropods, and is clearly far too high for Western Atlantic gastropods. This may reflect that most Western Atlantic workers have introduced names for full species; the tradition of naming varieties and forms is not as strong as it has been historically among European workers. Undoubtedly many species listed as valid will be synonymized once monographic work on particular families is done, but other species will be taken out of synonymy, and new species will continue to be discovered. Synonymy ratios for Western Atlantic gastropods are unlikely to significantly exceed 1:1.

Table 2. Composition of records in the Western Atlantic marine gastropod database.

CURRENTLY RECOGNIZED SPECIES			3988
	Tropical	3103	
	Caribbean	2164	
	Northern	413	
	Southern	472	
NOMINA DUBIA			157
SYNONYMS			4189
	validly published	3491	
	invalidly published	78	
	misidentifications	435	
	misspellings	185	
EXTRALIMITAL			36*
TOTAL RECORDS			8370

*includes one land snail erroneously described as marine.

Of the 3988 currently recognized species, 3103 (78%) occur in tropical or semitropical areas, here defined as extending from Cape Hatteras to Rio de Janeiro, Brazil (south of 35°N to north of 24°S). Of these, 2164 occur in, but are not necessarily restricted to, the Caribbean region (south of 24°N, north of 8°N; west of 59°W, east of 88°W). About 413 species are restricted primarily to northern areas (north of 35°N) and 472 to southern areas (south of 24°S).

The only estimate of the size of the entire Western Atlantic molluscan fauna appears to be that of Clench (1959), who predicted (without documentation) that it "would exceed 6,000 species and subspecies, but would not reach 8,000 species and subspecies." Abbott (1974) lists 4491 species of marine gastropods in the Americas (Western Atlantic and Eastern Pacific) and 1918 species in other classes, giving a ratio of 2.34 gastropods species per non-gastropod. The total of 3988 marine gastropods in the database therefore implies that there should be about 1700 non-gastropod mollusks in the Western Atlantic. Thus, known diversity of Western Atlantic mollusks is about 5700 species, substantiating Clench's prediction that total diversity will exceed 6,000 species as knowledge of the fauna increases.

The estimate of 3100 species of gastropods in the tropical Western Atlantic is considerably higher than previously thought. The tropical Western Atlantic molluscan fauna is usually considered less diverse than that of the tropical Eastern Pacific. Keen (1971:2) stated "at the moment, preliminary lists suggest that the Pacific side, in spite of its narrow continental shelf, has more species." However, Keen lists only 2438 species of gastropods named by 1971 in the tropical Eastern Pacific. Of the 3103 Western Atlantic species, 2641 had been named by 1971. Given the uncertainty in these numbers, the diversity levels of these faunas must be considered indistinguishable.

Although there has never been a reliable estimate of the diversity of Western Atlantic gastropods, a number of authors have discussed the impoverishment of the fauna as compared to the Eastern Pacific (Olsson, 1961; Woodring, 1966; Vermeij, 1978, 1991; Stanley and Campbell, 1981; Stanley, 1986). Olsson (1961:2) stated, "As compared to its richness in the Miocene, the present-day Caribbean mollusks appear strangely modified and greatly impoverished; on the other hand, the Panamic-Pacific molluscan fauna has remained fundamentally unchanged." Stanley and Campbell (1981) demonstrated that Pliocene faunas in the Western Atlantic were 70-80% extinct, whereas Pliocene faunas of California were only 30% extinct. They invoked the higher extinction rates in the Western Atlantic to explain the depauperate Recent fauna in the region.

As demonstrated here, the gastropod fauna of the tropical Western Atlantic is not depauperate compared to that of the tropical Eastern Pacific. Previous workers have been attempting to explain a myth. It is true that the Western Atlantic fauna has undergone substantial extinction, but it is not possible to demonstrate that this has led to an overall decline in diversity. Other processes, such as speciation and immigration must be balancing extinction (Allmon *et al.*, 1993). It is possible that the Western Atlantic fauna is depauperate in shallow water as compared to that of the Eastern Pacific, with greater diversity in deeper water, where there is considerably more continental shelf area than in the Eastern Pacific. This possibility would be easily testable if data on Eastern Pacific mollusks were available in database form.

WESTERN ATLANTIC GASTROPOD BIOGEOGRAPHY

Comparisons of the faunas in different parts of the Western Atlantic have been complicated by the different names and combinations in use for a given species. Different emphases in regional sampling cause further problems. In one area workers have concentrated on micromollusks, in another the deep water fauna is virtually unknown. The database approach allows standardization of faunal lists by cross-referencing synonyms and generic placements. Collecting biases can be accounted for by excluding particular size, depth, or taxonomic ranges.

Eight selected regions of the tropical Western Atlantic serve to demonstrate the value of databases for making faunal comparisons. These are eastern and western Florida, Yucatan, Panama, Jamaica, Puerto Rico, the Netherlands Antilles and northern Brazil. Table 3 summarizes the total number of shelled gastropod species in these faunas. Shell-less species have been excluded from the comparisons because of great variability in regional reporting: more than 10% of the Brazilian fauna falls in the shell-less category, but only 3% of the reported Panamanian fauna. Table 3 also gives totals adjusted for depth (species occurring in less than 50 meters) and size (species with maximum size greater than 5 mm). Table 4 shows for each

Table 3. Number of marine gastropod species in selected tropical Western Atlantic faunas, with restrictions by size and bathymetry to standarize faunal comparisons.

Region	Total shelled	depth <50m #	%	size >5mm #	%	<50m + >5mm #	%
Western Florida	709	590	.83	577	.81	468	.66
Eastern Florida	778	663	.85	623	.80	529	.68
Yucatan	594	528	.89	490	.82	431	.73
Panama	444	423	.95	353	.80	332	.75
Jamaica	443	432	.98	381	.86	370	.84
Puerto Rico	674	546	.81	542	.80	450	.67
Neth. Antilles	678	662	.98	491	.72	480	.71
Northern Brazil	709	593	.84	589	.83	492	.69

Table 4. Percentage of species in common among the tropical Western Atlantic faunas in Table 3. The percentage reflects the proportion of species in the smaller fauna not reported in the larger fauna. Numbers are calculated based on the species greater than 5 mm occurring in less than 50 meters (column 7 of Table 3). Numbers below and above the diagonal are identical; both sets are included for ease of use.

REGION	WFL	EFL	Yuc	Pan	Jam	PR	NA	NBr
Western Florida	–	.75	.66	.50	.51	.54	.47	.56
Eastern Florida	.75	–	.71	.64	.66	.67	.58	.62
Yucatan	.66	.71	–	.67	.69	.67	.63	.56
Panama	.50	.64	.67	–	.65	.72	.72	.60
Jamaica	.51	.66	.69	.65	–	.79	.77	.61
Puerto Rico	.54	.67	.67	.72	.79	–	.74	.67
Neth. Antilles	.47	.58	.63	.72	.77	.74	–	.59
Northern Brazil	.56	.62	.56	.60	.61	.67	.59	–

pair of faunas the percentage of species that the smaller fauna has in common with the larger one. This is the Simpson Index (Simpson, 1943), which is appropriate for large faunal lists corrected for sampling biases (Alroy 1992). Important sources of information and results concerning faunal composition for each of these areas are discussed below.

Western and Eastern Florida: Faunal lists for western and eastern Florida north of 25°N (i.e. excluding the Florida Keys) were compiled from Lyons (1989) and all papers on mollusks of Florida cited in the bibliography therein, Springer and Bullis (1956), Perry and Schwengel (1955), Maury (1922), and all papers on mollusks of Florida published in *Nautilus* in the last 70 years. Records from Dall (1927) are excluded because the Fernandina, Florida station is actually off Georgia. Uncertain records were checked by reference to the collections at ANSP.

Three-quarters of all species from western Florida are also known from eastern Florida. Diversity is higher in eastern Florida than western Florida, probably because of a greater diversity of habitats in the former. Eastern Florida has more reefal, hard substrate areas than western Florida, which has mainly soft bottom. Reefal habitats in western Florida are restricted to patchy areas off-shore, such as the Florida Middle Grounds (Lyons, 1976; Turgeon and Lyons, 1977; Hopkins *et al.*, 1977). Five of the seven faunal regions have lowest similarity with western Florida, reflecting the absence of shallow reefal habitat there that is available in the other areas. Western Florida is most similar to eastern Florida and Yucatan, the two areas closest to it geographically.

Yucatan: The faunal list for Yucatan (the entire Yucatan Peninsula) is derived mainly from Vokes and Vokes (1983). Additional records, mostly for deep water mollusks, come from Dall (1881, 1889a). Yucatan shows greater faunal similarity to eastern Florida (71%) than to western Florida (66%), although it is geographically closer to western Florida. Yucatan shares with eastern Florida a strong shallow-water reefal faunal component that is absent in western Florida.

Panama: The faunal list for Panama comes mainly from Olsson and McGinty (1958) and Radwin (1969). The few available records deeper than 50 meters come from Petuch (1990).

Jamaica: Records from Jamaica come primarily from Humfrey (1975), but species that he listed under "Other Jamaican Gastropods" on pages 198-205 were excluded unless confirmed by other sources. All of C.B. Adams' Jamaican marine gastropods as documented by Clench and Turner (1950) are included, synonymized as appropriate.

Puerto Rico: Puerto Rican records are taken mainly from Warmke and Abbott (1961), Ortiz-Corps (1983) and Dall and Simpson (1901). Many deep water records come from Watson (1886). Puerto Rico shows greatest faunal similarity to Jamaica (79%) and the Netherlands Antilles (74%), the two closest points among the regions compared here.

Puerto Rico and the Netherlands Antilles are about equidistant from northern Brazil but the Brazilian fauna is more similar to that of Puerto Rico (67%) than to that of the Netherlands Antilles (59%). Puerto Rico and the Netherlands Antilles share 74% of their species. Puerto Rico shares 62 species with northern Brazil that it does not share with the Netherlands Antilles. There is no obvious pattern in taxonomy or habitat preference among these species, but it is possible that they tend to be deeper water species. The average minimum depth for species occurring in less than 50 meters depth is between 3 and 4 meters in both Puerto Rico and the Netherlands Antilles. The species shared by Puerto Rico and Brazil but not the Netherlands Antilles have an average minimum depth of 9.5 meters. Collecting in moderate depths (10 to 50 meters) in the Netherlands Antilles should increase the apparent similarity with the Brazilian fauna.

Netherlands Antilles: The primary source of information is Jong and Coomans (1988). Virtually no information is available about deep-water mollusks of this region; only 3% of the gastropods known from the area are restricted to depths below 50 meters. On the other hand, the micromolluscan fauna is extremely well known because of the work of Jong and Coomans and their colleagues. About one quarter of the gastropod species reported from the Netherlands Antilles do not exceed 5 mm at maturity, a higher percentage than reported anywhere else in the Western Atlantic.

Northern Brazil: Because of the enormous extent of the Brazilian coastline, comparisons were restricted to northern Brazil. Only those species whose geographic ranges lie within or cross the zone from 4°N to 6°S (Amapá to Rio Grande do Norte) were included. The two primary sources are Rios (1985) and Leal (1991). Rios (1975) gave more precise station data than in 1985; Rios (1970) provided maps showing the locations of many stations. Leal (1991) documented the faunas of Atol das Rocas and Fernando de Noronha, which are included in this zone.

The average similarity of the Brazilian fauna to other tropical Western Atlantic faunas is 0.60, somewhat lower than the average similarities for the other areas, which range from 0.64 to 0.69 (except western Florida at 0.57).

This is consistent with its geographical remoteness from the Caribbean area.

Western Atlantic: Of 28 pairwise comparisons between eight Western Atlantic faunas, only a single one yields a similarity lower than 50%: that between western Florida and the Netherlands Antilles. All other values are above 50%, as expected for regions within a single biogeographic province. Of the 3103 gastropod species occurring in the tropical Western Atlantic province, 2497 (80%) are restricted to that region. Coomans (1962) defines a biogeographic province (which he calls an "autonomous zoogeographical province") as having at least 50% endemic species.

There seems to be little basis for recognizing biogeographic subprovinces within the tropical Western Atlantic, because similarities between regional faunas are determined as much by habitat availability as by geographic proximity. As shown in Table 5, no local region of the Western Atlantic has more than about 4% endemics, excluding species named since 1980 as these are likely to be discovered in other areas once attention has been called to their existence. Such low levels of endemicity are insufficient to make faunal province subdivisions. Coomans (1962) lumped the Virginian area (Cape Hatteras to Cape Cod) into the Boreal Province because it had only 10.5% endemic species.

Tropical Western Atlantic endemics are not concentrated in one area, although they appear more common on continental margins than on islands. Petuch (1990) named the Blasian faunal subregion for the Caribbean coast of Panama and Costa Rica, but Panama (including Costa Rica) has only about 4% endemic species (Table 5). Jong and Coomans (1988) named a number of species from the Netherlands Antilles increasing apparent endemicity, but many of these have been identified in samples from the Bahamas at ANSP (J. Worsfold, pers. comm.). Thus, even as our knowledge of regional Western Atlantic faunas increases, it is unlikely that the percentage of narrow ranging endemics will increase. Diversity in the tropical Western Atlantic is, however, higher than has been commonly perceived, and many local faunas have been badly under-sampled.

In 1901, Dall and Simpson estimated "the average American marine tropical shell-fauna" to contain about 600 species. Five of the eight faunas discussed here exceed 600 species of gastropods alone. A hint of the diversity yet to be discovered comes from the Worsfold collection at ANSP, which documents about 1550 species of Bahamian mollusks. Because most species in the tropical Western Atlantic are widespread, as indicated by the high similarities of the eight widely separated faunas studied here, diversity in the Bahamas should be considered typical of the faunal province as a whole. Most local faunas in the tropical Western Atlantic will eventually be demonstrated to have in excess of 1500 species of Recent marine mollusks.

Table 5. Number and percentage of endemic species in the faunas in Table 3. The second column repeats the totals from the seventh column of that table.

Region	<50m, >5mm	Endemic #	Endemic %
Western Florida	468	17	3.6
Eastern Florida	529	9	1.7
Yucatan	431	10	2.3
Panama	332	14	4.2
Jamaica	370	2	0.5
Puerto Rico	450	4	0.9
Neth. Antilles	480	14	2.9
Northern Brazil	492	14	2.8

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A bibliography of Caribbean malacology 1826 - 1993

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Abstract. A bibliography of over 800 publications lists major works on marine, land and freshwater mollusks, both Recent and fossil, occurring in the Caribbean Sea, its islands, and the bordering regions of Central and South America. Emphasis is placed on papers dealing with zoogeography and/or taxonomy, intended as an introduction to the molluscan fauna of this geographic area. A geographic index is provided.

This bibliography covers over 800 malacological publications for the Caribbean. It is a selected listing, admittedly incomplete, but intended to provide access to the main body of literature in this field.

Geographic coverage includes the Caribbean Sea and its islands, as well as the bordering regions of Central and South America. Western and eastern borders are defined by the eastern edge of the Yucatan Peninsula and the island of Barbados. The northern coasts of Cuba and Hispaniola are also included. Florida and the Bahamas are not included. The coverage extends to marine, land and freshwater mollusks, both Recent and fossil. The inclusion of some parts of Central and South American land masses, and the treatment of fossils from several periods, make this a very general concept of "Caribbean."

Emphasis is placed on malacological papers dealing with zoogeography and/or taxonomy relevant to this geographic area. Taxonomic treatments were generally included only if they covered taxa at the generic level or above, i.e. papers dealing with only one or a few species were not included. Exceptions to this rule were small parts of a large series of papers by a single author or authors. Large monographs including the Caribbean but covering a much wider area (e.g. world-wide treatises) normally were not included. Abstracts and theses were listed only if they provide useful information which has not been formally published. In all cases, we were more lenient with older literature, papers dealing with areas otherwise not covered, and "obscure" works. Entries are organized alphabetically by authors. A geographic index is also provided. Geographic areas are listed in brackets following the reference only if not apparent by the title of the work.

In the interest of space, we have not included the contents of the journal *Johnsonia* (*Monographs of the Marine Mollusks of the Western Atlantic)*, published in 50 parts between 1941 and 1974 by the Department of Mollusks, Museum of Comparative Zoology, Harvard University. Likewise, only selected works have been included from the numerous malacological publications produced in Panama, Venezuela, and Cuba (see Bieler and Kabat, 1991), e.g. the *Revista de la Sociedad Malacólogia "Carlos de la Torre"* (see published index to the last, Jacobson, 1971). These essential references should be consulted for additional information on the mollusks of this region. The abstract volume for the Primer Congreso Latinoamericano de Malacologia, 15-19 July 1991, Universidad Simón Bolivar, Caracas, Venezuela, also provides many useful references.

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- **Dominican Republic** (= Santo Domingo, San Domingo): Aguayo 1949b; Clench 1938, 1962b; Crosse 1891a-c; Gabb 1871, 1873, 1875; Gomez *et al.* 1986; Hjalmarson and Pfeiffer 1858; Ingram 1939; Jung 1986; Jung and Petit 1990; Maury 1917; J. C. Moore 1850, 1853; Pflug 1961; Pilsbry 1922, 1933; Pilsbry and Johnson 1917; Pilsbry and Olsson 1954; Pilsbry and Sharp 1898; Poinar and

Roth 1991; Ramírez 1950, 1956; Saunders *et al.* 1986; Vanatta 1914; E. H. Vokes 1979, 1989; H. E. Vokes 1989; Vokes and Vokes 1992; E. H. Williams *et al.* 1983.

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Virgin Islands: Eddison 1964; Ferguson and Richards 1963; Maes 1983; Marcus and Marcus 1962; Maury 1920; McLean 1951; Voss 1958; Weber 1961.

St. Croix: Bland 1881; Faber 1988; Gladfelter 1974; Jacobson 1968; A. I. Miller 1989; Mörch 1863; D. R. Moore 1972; Nowell-Usticke 1956, 1959a, b, 1961a, b, 1963a, b, 1968, 1969, 1971; Old 1979; P. Williams 1985.

St. John: Muchmore 1993; Woodlock 1963, 1964, 1965, 1966.

St. Barthélemy: Nowell-Usticke 1961c.

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Lesser Antilles - Leeward Islands: Adam 1957; Cooke 1919; Gerth 1951; Hummelinck 1940d; Nowell-Usticke 1968; Nutting 1919; Vaughan 1919.

Antigua: Brown 1913; Brown and Pilsbry 1914; Merian 1844; Nutting 1919; Pilsbry and Brown 1914; Schuster and Bode 1961.

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Saba: Clench 1970; Knudsen 1982.

St. Eustatius: van Regteren Altena 1961.

St. Christopher (= St. Kitts): Rush 1891; van Regteren Altena 1961.

St. Martin: Coomans 1963a,b, 1967, 1974.

Lesser Antilles - Windward Islands: Adam 1957; Gerth 1951; Guyard *et al.* 1982; Nowell-Usticke 1968; Nutting 1919; Sutty 1986; Vaughan 1915-1920.

Barbados: Conde 1966; Edmunds and Just 1983, 1985; Ferreira 1985; Jung 1968; Kidd and Sander 1979; Kugler *et al.* 1984; Lewis 1960, 1965; Lewis and Fish 1969; Marcus and Hughes 1974; Nutting 1919; Rush 1891; Sander and Lalli 1982; Senn 1940; Trechmann 1925b; Wells 1975.

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Martinique: Beau 1858; Bordaz 1899; Cossmann 1913; Dreyfuss 1953; Guppy 1913; Guyard and Pointier 1979; Lamy 1929; Mazé 1874; Starmühlner 1984; Starmühlner and Therezien 1983.

St. Lucia: Crosse and Bland 1873.

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Venezuela: Almeida 1974; Arocha and Urosa 1982; Arocha *et al.* 1991; H. B. Baker 1923-1930; Beauperthuy 1967; Bullis 1964; Ernst 1878; Flores 1964, 1966, 1968, 1973; Gibson-Smith 1973; Gibson-Smith and Gibson-Smith 1971, 1974, 1979, 1982b, 1983; Gonzalez and Flores 1972; González and Princz 1979; Guppy 1873a, 1913; Hodson 1926; Hodson and Hodson 1931; Hodson *et al.* 1927; Hubendick 1961; Hummelinck 1940a-c; Ingram 1947; Jung 1965, 1973, 1975; Lorié 1889; Marks 1952; Martens 1873; A. K. Miller and Thompson 1937; Olsson 1942; Palmer 1945; Petuch 1976, 1981a; Princz 1973, 1980, 1982, 1983, 1987; Princz and González C. 1981; Princz and Gonzalez de Pacheco 1981; Rehder 1962a; H. G. Richards and Wagenaar Hummelinck 1940; Rodríguez 1959; Rutsch 1934b; Schenck 1935; Schilder 1939; Sutton 1946; Talavera and Princz 1984; Tello 1975; F. G. Thompson 1957; van Benthem Jutting 1945; Weisbord 1962, 1964a, b; Work 1969.

Netherlands Antilles: H. B. Baker 1924; Coomans 1958, 1961, 1974; De Jong and Coomans 1988; Engel 1936; Hummelinck 1940b, c; Nowell-Usticke 1962; Seamon and Seamon 1967; van Kuyp 1949, 1951; Vernhout 1914; Vries 1974.

Aruba: Lorié 1889.

Bonaire: Adam 1937; Moolenbeek and Faber 1984.

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Panama (Atlantic): C. B. Adams 1852a; Aguayo 1949a; Bartsch 1931; Brattström 1985; Brown and Pilsbry 1911-1913a, 1913b; Carpenter 1863; Cossmann 1913; Cubit and Williams 1983; Dall 1912a, b; Glynn 1970; Jackson and Jung 1992; Jackson *et al.* 1993; Keen and Thompson 1946; MacDonald 1919; Marcus and Marcus 1967; Meyer 1977; Nicol 1945; Olsson 1942, 1972; Olsson and McGinty 1958; Petuch 1990; Pilsbry 1910a, 1920c, 1926b, 1930b; Radwin 1969; Rehder 1942; Rosewater 1975, 1976; Toula 1909-1911; Vaughan 1919; Vermeij and Petuch 1986; E. H. Vokes 1983; Woodring 1957-1982, 1966; Woodring and Thompson 1949.

Costa Rica (Atlantic): Bakus 1968; Dall 1912a; Gabb 1881b; Gómez and Valerio 1971; O. Haas 1942; Houbrick 1968; Kemperman and Coomans 1984; Nicol 1945; Olsson 1922; Palmer 1923; Pilsbry 1911, 1920a, c, 1926a; Pittier 1890; Rehder 1942; Robinson 1991, 1993; Robinson and Montoya 1988.

Nicaragua (Atlantic): Bock and Moore 1971; Fluck 1900, 1901, 1905-1906; H. G. Richards 1939; Tate 1870.

Honduras (Atlantic): Ancey 1886; Boone 1925; Britton 1976; Clapp 1914; E. F. Garcia 1988; F. Haas 1941; F. Haas and Solem 1960; Petuch 1981b; Pilsbry 1930a; H. G. Richards 1938; Robertson

Guatemala (Atlantic): Fischer and Crosse 1870-1900; Goodrich and van der Schalie 1937; Hinkley 1920; Pilsbry 1920b, c.

Belize: Boone 1925; K. B. Clark and De Freese 1987; Rützler and Macintyre 1982.

Mexico (Yucatan Peninsula, Caribbean coast): F. C. Baker 1891; Bequaert and Clench 1933, 1936, 1938; Bergh 1890; Branson and McCoy 1963; Carnes 1975; Ekdale 1972, 1974; Fischer and Crosse 1870-1900; González *et al.* 1991; F. Haas 1941; Harry 1950; Hidalgo 1956; Jaume 1946; Kornicker *et al.* 1959; D. R. Moore 1973; Perrilliat 1981; Pilsbry 1891, 1920b, c; Rehder 1966; Rehder and Abbott 1951; Rice and Kornicker 1962, 1965; H. G. Richards 1937; Strebel 1873-1882; Treece 1980; H. E. Vokes 1983; Vokes and Vokes 1984; Weisbord 1926.

ACKNOWLEDGMENTS

For assistance in literature acquisition, we are indebted to Librarians Kristen Metzger and Marilyn Morris and volunteer Marguerite Repass, all of Harbor Branch Oceanographic Institution. Dr. Gary Rosenberg (Academy of Natural Sciences, Philadelphia) offered a number of useful additions to the manuscript. This is Harbor Branch Oceanographic Institution Contribution no. 970 and contribution no. 335 of the Smithsonian Marine Station at Link Port.

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Date of manuscript acceptance: 16 July 1993

BOOK REVIEW

Field Guide to Freshwater Mussels of the Midwest

Illinois Natural History Survey Manual 5. Kevin S. Cummings and Christine A. Mayer.
Illinois Natural History Survey, Champaign, Illinois. 1992. 194 pp. $15.00

This manual, intended for aquatic biologists and amateur naturalists, fills a recognized void in practical identification guides to the freshwater mussels. Current guides to mussels are of limited value to frustrated novices with bags of shells not readily identified by line drawings in the national and state-level keys available, but difficult to procure. The nearly pocket-sized guide provides coverage of 78 species arranged in systematic order. Using the assumption that nearly all midwestern mussels can be identified by written descriptions and especially color photographs, with concurrence from range maps, the authors provide a key to subfamilies followed by species accounts, with nomenclature largely following Turgeon *et al.* (1988). The matching of valves in hand to those in color plates provides a simple and largely effective means to identify most species likely to be collected. Problematic taxa, such as pigtoes of various sizes and rivers of origin, will continue to befuddle even the most astute conchologists.

Species accounts consist of one-page narratives arranged as follows: common and scientific name, other common names, key characters, similar species, description, habitat and status. The opposing page contains a color photo of the external valve and a range distribution map for the Midwest. Photos depict representative specimens, with sexually dimorphic species represented by both sexes. The pictorial guide will facilitate comparison of collected valves to identified species; a conchological "match the catch". Inclusion of key characters and a list of look-alikes makes this guide very user friendly to all collectors. Because the range maps portray historic distributions only, they are marginally useful to nonspecialists. For example, the winged mapleleaf probably consists of a single population in the St. Croix River, Wisconsin, yet the map shows it to be widespread in seven states. Additional accounts on fingernail clams, asian clam, and the zebra mussel cover the other bivalves likely to be collected with unionids.

The text's education message on status of this molluscan family in the Midwest is clear; more than 50% of species are threatened or endangered throughout their range or in various states where they reside. The colorful and conspicuous native mussels in all rivers are in deep trouble because of habitat loss and degradation, and on a collision course with the invading zebra mussel. This reasonably priced field guide is a valuable diagnostic and instructional tool for all mussel enthusiasts, and it will hopefully serve as a model for any future state or regional keys.

–Richard J. Neves
Virginia Tech.
Blacksburg, Virginia

AMERICAN MALACOLOGICAL UNION FINANCIAL REPORT

1992 Income and Expenses

Income:

1990 & 1991 Dues (all categories)	$ 60.00
1992 Dues (all categories)	5,801.00
1993 Dues (all categories)	2,723.00
Bulletin Subscriptions - Volume 8	134.00
Bulletin Subscriptions - Volume 9	337.00
Bulletin Subscriptions - Volume 10	1,954.00
Bulletin Subscriptions - Volume 11	645.00
Bulletin back issues & Supplements	1,153.65
Page charges and reprints [Vol. 9(1) & (2)]	2,726.24
Other publications	187.00
T-shirt sales	28.00
Student Award Donation	250.00
Auction	608.00
Interest (all accounts)	5,926.45
Miscellaneous income	156.87
Symposium Fund Donations	459.00
TOTAL	$ 23,149.21

Expenses:

Office expenses	407.45
Printing	421.09
Telephone and Postage	688.23
Dues in other organizations	265.00
California Franchise Fee	15.00
Insurance and Bond	391.00
Accounting	125.00
Travel expenses	837.54
Symposium expenses	2,825.00
Student Paper Awards	750.00
Bulletin 9(1) and AMU News 22(3)	8,451.36
Bulletin 9(2)	8,711.24
AMU News 23(1)	882.09
AMU News 23(2)	1,075.62
Envelopes (Shaughnessy Press)	233.97
Taxes withheld	11.30
TOTAL	$ 26,090.89

Decrease in cash assets	(2,941.68)
Cash assets as of 1/1/92	$ 98,041.96
Cash assets as of 1/1/93	$ 95,100.28

60th ANNUAL MEETING
THE AMERICAN MALACOLOGICAL UNION
HOUSTON, TEXAS
JULY 9 - 14, 1994

The 1994 meeting of the American Malacological Union will be held at the Hyatt Regency Houston in the center of downtown Houston, Texas. The meeting will begin with the President's "Taste of Texas" reception and will include a workshop on unionids, contributed papers and posters, the annual auction of books and shells, and a dealers' bourse. Social events will include a barbecue at a Texas ranch and a fiesta evening at the Houston Museum of Natural Science. In addition, the collections of the Houston Museum will be available for inspection by meeting attendees.

A special symposium on "The Mollusca of the Gulf of Mexico" will be chaired by Drs. Joseph C. Britton, Texas Christian University and John W. Tunnell, Jr., Corpus Christi State University.

Field trips, scheduled for July 14 will include outings to a Gulf beach, a fossil site, freshwater streams and the Marine Biomedical Institute at Galveston.

Hotel accommodations at the Hyatt Regency are as follows: single or double occupancy $73.00; triple occupancy $89.00; quadruple occupancy $99.00. The Hyatt Regency is conveniently located in the heart of downtown Houston, near to many restaurants and access to tunnel shops. Also, daily van trips to the Galleria and shopping malls will be provided, as well as to the Houston Museum of Natural Science.

Don't miss what promises to be one of the most fun and exciting AMU meetings!

For further information please contact:
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President, AMU
Malacology Department
Houston Museum of Natural Science
1 Hermann Circle Drive
Houston, Texas 77030
(713) 639-4677 (phone)
(713) 523-4125 (FAX)

IN MEMORIAM

C. Clifton Coney
Vera Fretter
Richard S. Houbrick

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CONTRIBUTOR INFORMATION

The *American Malacological Bulletin* serves as an outlet for reporting notable contributions in malacological research. Manuscripts concerning any aspect of original, unpublished research, important short reports, and detailed reviews dealing with molluscs will be considered for publication.

Each original manuscript and accompanying illustrations must be submitted with two additional copies for review purposes. Text must be typed on one side of 8-1/2 x 11 inch bond paper, double-spaced, and all pages numbered consecutively with numbers appearing in the upper right hand corner of each page. Leave ample margins on all sides.

Form of the manuscript should follow that outlined in the *Council of Biology Editors Style Manual* (fifth edition, 1983). This can be purchased from the CBE, 9650 Rockville Pike, Bethesda, Maryland 20814, U.S.A.

Text, when appropriate, should be arranged in sections as follows:

1. Cover page with title, author(s) and address(es), and suggested running title of no more than 50 characters and spaces. Authors should also supply five key words, placed at the base of this page, for indexing purposes.
2. Abstract (less than 5 % of manuscript length)
3. Text of manuscript starting with a brief introduction followed by methodology, results, and discussion. Separate sections of text with centered subtitles in capital letters.
4. Acknowledgments
5. Literature cited
6. Figure captions

All binomens must include the author attributed to that taxon the first time the name appears in the manuscript [e.g. *Crassostrea virginica* (Gmelin)]. This includes non-molluscan taxa. The full generic name along with specific epithet should be written out the first time that taxon is referred to in each paragragh. The generic name can be abbreviated in the remainder of the paragraph as follows: *C. virginica.*

References should be cited within text as follows: Hillis (1989) or (Hillis, 1989). Dual authorship should be cited as follows: Yonge and Thompson (1976) or (Yonge and Thompson, 1976). Multiple authors of a single article should be cited as follows: Beattie *et al.* (1980) or (Beattie *et al.*, 1980).

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Beattie, J. H., K. K. Chew, and W. K. Hershberger. 1980. Differential survival of selected strains of Pacific oysters *(Crassostrea gigas)* during summer mortality. *Proceedings of the National Shellfisheries Association* 70(2):184-189.

Hillis, D. M. 1989. Genetic consequences of partial self-fertilization on population of *Liguus fasciatus* (Mollusca: Pulmonata: Bulimulidae). *American Malacological Bulletin* 7(1):7-12.

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Yonge, C. M. and T. E. Thompson. 1976. *Living Marine Molluscs.* William Collins Son & Co., Ltd., London. 288 pp.

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Any manuscript not conforming to *AMB* format will be returned to the author for revision.

Final submission of accepted, revised manuscripts should include two typed copies of the text, tables, etc. and an additional copy in electronic form on 3.5" diskette. The electronic version should be readable as non-formatted ASCII files.

New Taxa. The *Bulletin* welcomes complete descriptions of new molluscan taxa. Establishment of new taxa must conform with the International Code of Zoological Nomenclature (1985). Descriptions of new species-level taxa must include the following information in the order as given: higher taxon designation as needed for clarity; family name with author and date; generic name with author and date; *Genus species* author sp. *nov.* followed by numeration of all figures and tables; complete synonymy (if any); listing of type material with holotype and any other type material clearly designated along with complete museum catalogue or accession information; listing of all additional non-type material also with full museum deposition information;

type locality; diagnosis and full description of material done in telegraphic style including measurements and zoogeographic distribution as necessary; discussion; etymology. Descriptions of new supraspecific taxa should include type species (for new genus) or type genus (for new family), diagnosis and full description done in telegraphic style, and list of included taxa.

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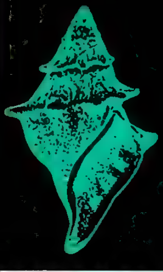

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EDITORIAL COMMENT

With this issue, the *American Malacological Bulletin* begins its second decade of publishing original research in the field of malacology. This issue also marks the first *Bulletin* without Dr. Robert S. Prezant as Editor-in-Chief. In his final editorial comments that appeared in volume 10(2) of the *AMB*, Bob provided a brief history of the development and growth of the *Bulletin* during his tenure as founding Editor. He also noted the contributions of the many persons who helped to create, sustain, and build this publication. However, no historical review of the *AMB* can be complete without mention of Bob's immense contribution to this journal.

In many ways, Robert Prezant symbolized the *AMB* during its first decade. His stewardship, guidance, editorial skills, perseverance, and fiscal resourcefulness gave life to the *Bulletin*, nurtured it during its early years, and helped to establish it as an internationally recognized, peer-reviewed journal dedicated to the pursuit of scholarly research on the Mollusca. It was my privilege to serve with Bob as his Managing Editor beginning with volume 5(1). His skill as a mentor will always be appreciated.

It is not an overstatement to say that the *American Malacological Bulletin* owes its inception and continued steady growth and development to Robert S. Prezant. His many talents and skills combined with a keen sense of humor, particularly in the face of nearing deadlines, made him an invaluable asset. His innumerable contributions will always be remembered as the current editor seeks to continue the high level of professional standards that he brought to this position.

Ronald B. Toll
December 1994

Form and function of unionoidean shell sculpture and shape (Bivalvia)

G. Thomas Watters

Aquatic Ecology Laboratory, Department of Zoology, Ohio State University, 1314 Kinnear Road, Columbus, Ohio 43212, U.S.A.

Abstract. The functions of Recent and fossil unionoidean sculpture are proposed in light of similar theories on the function of marine bivalve sculpture. Functional models are given for shell morphologies for both soft and hard substrata. Most soft substratum taxa have shells of reduced thickness and dentition, are laterally compressed, and generally are sculptureless. These characteristics minimize the specific gravity of soft substratum unionoideans. Sculptured taxa generally are found in hard substrata in large rivers. Shell sculpture is derived from an ancestral divaricate pattern, and has been modified into the spectrum of unionoidean sculpture found in Recent and fossil species. Shell sculpture in this group is modified for anchoring and anti-scouring functions. Burrowing sculpture, found in many marine bivalves, may not occur in unionoideans, but was exapted from ancestral burrowing sculpture for other roles. Big river taxa have evolved mechanisms for remaining buried, while headwater species have emphasized the ability to rebury if dislodged. It is proposed that unsculptured big river taxa evolved in headwater situations and reinvaded large rivers with alternate methods to facilitate anchoring and reduce scour. These methods form the morphological facies known as the "Big River Effect."

In a series of articles, Stanley (1969, 1970, 1972, 1975a, 1977b, 1981) documented the probable function of many types of marine bivalve shell sculpture. These involved the exaptation (*sensu* Gould and Vrba, 1982) of preexisting sculpture for new tasks. He also introduced the idea of composite sculpture, where sculpture on different areas of the shell could serve different functions. Spines, ribs, and scales would never again be considered ornamentation. They were devices with a function. Mark Twain's 1874 observation that "architects cannot teach nature anything" was being demonstrated by morphologists a century later.

One major bivalve group, the freshwater "mussels" of the Unionoidea, largely has been omitted from the discussion of the functional morphology of shell sculpture, although this group has some of the most highly developed sculpture in the class. Although some authors (*e.g.* Savazzi and Peiyi, 1992) have suggested functional roles for unionoidean sculpture, no study has addressed these bivalves comprehensively.

It is proposed here that unionoidean sculpture is derived from ancestral trigonoidean sculpture and acts as anchors and anti-scouring devices. Three types of anchors were found. The generalized anchor is the most prevalent and consists of pustules dispersed over the disc of the shell. The medial anchor is composed of a radiating area of pustules, knobs, or spines across the shell. The third type, referred to here as the U2-D2 anchor, consists of undulating ribs aligned obliquely to the burrowing axis. These anchors are compared with shell sculpture patterns evaluated by other workers for burrowing sculpture. These patterns entail allometric densing, perimeter smoothing, frictional asymmetry, and cross-orientation, described below.

METHODS

Four species of unionids were used to test hypotheses of the sculpture function: *Amblema plicata* (Say, 1817), *Obliquaria reflexa* Rafinesque, 1820, *Quadrula pustulosa* (Lea, 1831), and *Cyclonaias tuberculata* (Rafinesque, 1820). These represent common and widespread species that occur in various habitats. *Cyclonaias* was taken from the Green River at Munfordville, Kentucky, in 0.3 m of water in a swift run. The remaining three species were taken from a mussel bed at Devola in the Muskingum River, Ohio, in 4 m of water in a moderate current. *O. reflexa* represents an example of a well-defined medial anchor of alternating knobs. The form of *Q. pustulosa* used has a weakly formed medial anchor of low, small pustules. *C. tuberculata* represents an example of a well-developed generalized anchor composed of prominent pustules scattered over the disc of the shell. *A. plicata* is an example of a species having a U2-D2 anchor.

Shells were notched on the anterior, dorsal, and ventral margins, and filled with a ceramic-like compound (Super Sculpey^{TM}, Polyform Products Co.). The total weight approximated that of the shell and animal when alive. Eye screws (6.35 mm length) were inserted in the compound at the notches (Fig. 1). The shells then were baked at 132°C for 20 min to harden the compound. The

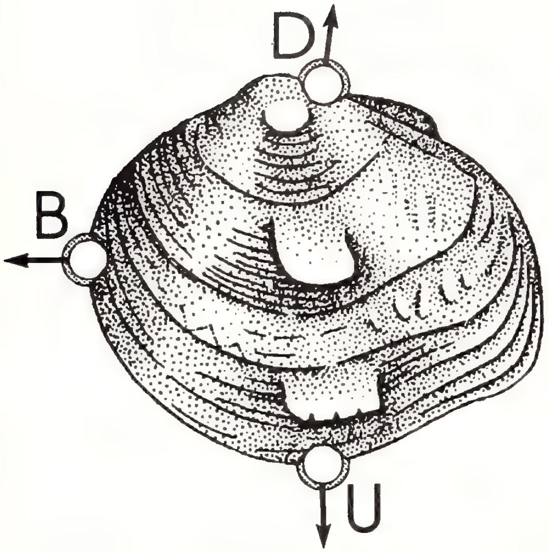


Fig. 1. Shell fitted with eyelets for measuring drag along three directions: B, burrowing; D, umbo downstream; U, umbo upstream (shell after Kuester, 1858-1859).

weights and dimensions (length x height x width) after treatment were: *Amblema plicata*, 40.9 g, 52 x 39 x 27 mm; *Obliquaria reflexa*, 31.5 g, 45 x 35 x 23 mm; *Quadrula pustulosa*, 62.0 g, 51 x 50 x 33 mm, and *Cyclonaias tuberculata*, 40.6 g, 45 x 35 x 23 mm. A 16 lb steel fishing leader was attached to the anterior eyelet and looped through a pulley to a Homs Model 200G piston-type scale (200 g). The shell was buried in sediment to the shell margin in all runs. Substrates were covered with a 2 cm layer of water. Force was exerted uniformly (pulled) on the scale until the shell was dislodged from the substratum. Because weight is a force, and all shells were pulled for the same distance, the unit grams can be used as a comparative measure of work. The grams necessary for dislodgment were recorded and the experiment repeated for a total of ten replicates per shell position. Three shell positions were used: 1) posterior to anterior, 2) ventral to dorsal, and 3) dorsal to ventral. The first orientation simulated burrowing, the latter two positions dislodgment by currents. Two sediment types were used: medium to fine sand (< 0.42 mm grain diameter); and a mixture of pebbles (41%), very coarse sand (40%), coarse sand (10%), and medium to fine sand (9%), based on dry sieve weight, taken from the Muskingum River where the specimens of *A. plicata, O. reflexa* and *Q. pustulosa* were found. To compare the effects of sculptured versus sculptureless shells in these sediments, the sculpture was filed off the specimens and the tests conducted again. To lessen the effects of reduced weight due to removal of the sculpture, specimens were weighed before and after smoothing, and the difference added to the results of the smoothed results. Means were compared with a t-test.

Anchoring and burrowing drag were compared between similar size headwater and big river morphs of *Fusconaia flava* (Rafinesque, 1820). The headwater specimens were from Big Darby Creek (Scioto River drainage, Ohio), from a shallow riffle-run, and the big river specimens were from the Mississippi River main channel near Rock Island, Illinois. Ten individuals of each group were tested as above for resistance to burrowing and anchoring. Anchoring was measured with the umbo downstream, the most common orientation for this species in a current.

The angle of the medial anchor sculpture was measured from a line tangent with the hinge line (Fig. 2) for 21 species. The results were fit to 5° increments and transformed to percentages. The angle of the U2-D2 arms was measured similarly (Fig. 3) for five species.

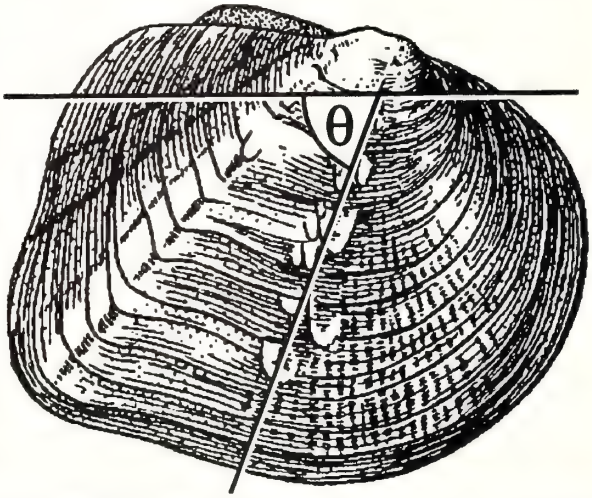


Fig. 2. Method for measuring angle of medial anchor (θ) (shell after Kuester, 1858-1859).

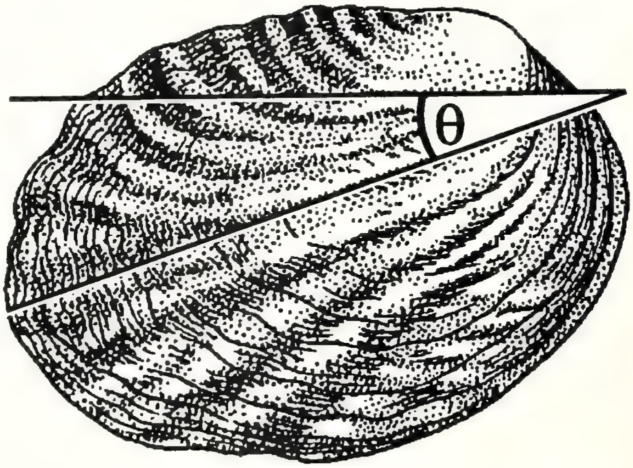


Fig. 3. Method for measuring angle of U2-D2 arm (θ) (shell after Kuester, 1858-59).

Allometric densing occurs when the size of sculptural elements (ribs, knobs, etc.) do not enlarge at the same rate as the rest of shell, resulting in relatively smaller sculpture in large shells when compared to smaller ones. Four species were used to test the hypothesis that anchoring sculpture displays allometric densing: *Amblema neisleri* (Lea, 1858); *Obliquaria reflexa; Plectomerus dombeyana* (Valenciennes, 1827); and *Plethobasus cicatricosus* (Say, 1829). The position of the sculpture along a growth vector (distance across shell surface from umbo to sculpture) was plotted versus the interval between sculpture apices. Some early sculpture may have been eliminated by natural abrasion. These results were fitted to the allometric equation, and the derived exponent k was compared graphically with the theoretical isometric value of $k = 1$.

Two species were used to test the hypothesis that unionoideans have anti-scouring sculpture: *Quadrula quadrula* (Rafinesque, 1820) and *Tritogonia verrucosa* (Rafinesque, 1820). Both species have well-developed dorsal costations. This sculpture was filed from the right valve of each species, although not all could be removed from *T. verrucosa* without penetrating the shell. The specimens were filled with compound and placed with anterior end oriented upstream and buried to the depth of the costations in a 5 cm/sec current. Medium to fine sand (< 0.42 mm grain diameter) was deposited evenly over the protruding shell and left for 10 min. The specimens were photographed at that time. This method is similar to that used by Stanley (1981) to illustrate an anti-scouring function for the sculpture of marine bivalves, and is strictly qualitative.

RESULTS

The well-developed generalized anchor of *Cyclonaias tuberculatus* was shown to increase drag in both anchoring directions (umbo upstream and downstream) in both substrata over a shell with the anchor removed (Table 1). A concomitant increase in drag along the burrowing direction was evident only in sand, and the anchor was most efficient in the sand and gravel mixture of its native Muskingum River mussel bed. The substrate in the Green River where the specimen was found was similar to that of the Muskingum River. Since this species is often found in nearly homogeneous coarse sand in other areas, future studies might compare shells from those two substrate types.

The well-developed medial anchor of *Obliquaria reflexa* also was effective in both orientations and in both substrata (Table 2), but increased burrowing drag in both substrata. It was slightly more efficient in the sand and gravel mixture of its native bed substratum.

The weakly-developed medial anchor of *Quadrula pustulosa* was not as effective as either the well-developed medial or generalized anchors (Table 3). In the sand and gravel mixture it was more effective with the umbo downstream (the most common life position) than with the umbo upstream. The reverse was true in sand, where it was most effective with the umbo upstream. An increase in burrowing drag was most evident in sand, and overall the anchor was most efficient in the native mixture.

The U2-D2 anchor of *Amblema plicata* was effective in both orientations and in both substrata (Table 4), but increased burrowing drag in sand. It was slightly more efficient in the sand and gravel mixture of its native bed substratum.

A comparison of headwater and big river forms of *Fusconaia flava* showed that the burrowing drag and anchoring drag of the big river form is significantly greater than that of the headwater form. The burrowing drag is significantly greater than the anchor drag in the big river morph, but not in the headwater morph (at p = 0.05).

Table 1. Comparison of burrowing and anchoring drag in sculptured and smoothed shells of *Cyclonaias tuberculatus* in sand and sand/gravel mixture. Values above the diagonal are t-test results. Values below the diagonal are levels of significance (p) for the t-test values. *** - p < 0.001; ** - 0.01 > p ≥ 0.001; * - 0.05 > p ≥ 0.01; NS - p ≥ 0.05 [not significant]. (B, burrowing orientation; D, umbo downstream; U, umbo upstream). Mean in grams.

			Sculptured						Smoothed					
			Sand & gravel			Sand			Sand & gravel			Sand		
			B	D	U	B	D	U	B	D	U	B	D	U
S	Sand & gravel	B		-1.5923	-0.0523	6.1571	7.0201	7.7948	-0.1233	1.0878	3.6062	7.1741	8.2272	9.2466
c		D	NS		2.2294	15.8611	18.3358	19.5572	1.7960	4.0181	7.9420	18.9738	20.7972	22.3176
u		U	NS	*		9.6690	11.2030	12.3206	-0.0952	1.5493	4.9667	11.5264	13.0927	14.5324
l	Sand	B	***	***	***		2.4071	4.6584	-8.0650	-7.6930	-3.2308	2.9017	6.0530	8.7393
p		D	***	***	***	*		2.6518	-9.2409	-9.1769	-4.4795	0.4441	4.1453	7.2317
t		U	***	***	***	***	*		-10.1987	-10.3281	-5.7957	-2.3737	1.2633	4.4142
S	Sand & gravel	B	NS	NS	NS	***	***	***		1.4620	4.4775	9.4688	10.7888	12.0377
m		D	NS	***	NS	***	***	***	NS		3.4278	9.4788	11.0801	12.5642
o		U	**	***	***	**	***	***	***	**		4.8275	6.4910	8.0620
o	Sand	B	***	***	***	**	NS	*	***	***	***		3.9436	7.1761
t		D	***	***	***	***	***	NS	***	***	***	**		3.3916
h		U	***	***	***	***	***	***	***	***	***	***	**	
		mean	84.4	95.6	84.8	43.4	38.2	32.8	85.4	76.2	57.2	37.4	30.2	23.0

Table 2. Comparison of burrowing and anchoring drag in sculptured and smoothed shells of *Obliquaria reflexa* in sand and sand/gravel mixture. Explanation as in Table 1.

			Sculptured						Smoothed					
			Sand & gravel			Sand			Sand & gravel			Sand		
			B	D	U	B	D	U	B	D	U	B	D	U
Sculpt	Sand & gravel	B		-4.1389	-2.7784	20.8825	21.3674	15.9852	13.8360	8.1172	12.3375	21.6800	21.3384	25.1743
		D	***		2.2099	20.7793	20.6945	17.1120	15.4540	10.7429	14.3269	21.5800	21.2473	23.4915
		U	*	*		27.6648	29.9217	21.3789	18.6306	11.2447	15.8441	27.9897	27.8069	34.5828
	Sand	B	***	***	***		-2.7724	-4.6208	-6.3131	-8.8523	-4.1318	2.2409	1.3828	2.5587
		D	***	***	***	*		-3.0148	-5.0333	-7.9573	-2.8323	5.1243	4.2287	7.6453
		U	***	***	***	**	**		-1.8053	-5.2087	-0.6748	6.3873	5.6960	7.6948
Smooth	Sand & gravel	B	***	***	***	***	***	NS		-3.6597	0.7566	7.9119	7.2811	9.3775
		D	***	***	***	***	***	***	**		3.8281	10.0947	9.5982	11.1359
		U	***	***	***	**	NS	NS	NS	**		5.5525	4.9913	6.0290
	Sand	B	***	***	***	*	***	***	***	***	***		-0.8581	-0.3548
		D	***	***	***	NS	***	***	***	***	***	NS		0.7385
		U	***	***	***	*	***	***	***	***	***	NS	NS	
		mean	95.4	114.6	105.0	28.2	33.8	40.8	46.4	61.0	43.4	22.2	24.6	23.0

Table 3. Comparison of burrowing and anchoring drag in sculptured and smoothed shells of *Quadrula pustulosa* in sand and sand/gravel mixture. Explanation as in Table 1.

			Sculptured						Smoothed					
			Sand & gravel			Sand			Sand & gravel			Sand		
			B	D	U	B	D	U	B	D	U	B	D	U
Sculpt	Sand & gravel	B		-3.7770	-0.1378	7.1815	9.7654	8.4873	-0.7683	1.3152	1.4963	6.5008	10.4324	12.9945
		D	**		3.8850	10.7732	13.1423	11.9804	3.0716	4.8421	5.5343	9.9638	13.6943	15.9261
		U	NS	**		8.2396	11.4022	9.8127	-0.6882	1.5347	1.8077	7.2894	12.0964	15.1817
	Sand	B	***	***	***		3.2685	1.5787	-8.1196	-5.1053	-6.8936	0.0000	4.4491	8.5357
		D	***	***	***	**		-1.7356	-10.7715	-7.3096	-10.4157	-2.5239	1.7108	7.0648
		U	***	***	***	NS	NS		-9.4583	-6.2299	-8.6208	-1.2657	3.1247	7.7232
Smooth	Sand & gravel	B	NS	**	NS	***	***	***		2.0471	2.3687	7.3522	11.4196	14.0082
		D	NS	***	NS	***	***	***	NS		-0.0688	4.6768	7.9763	10.2409
		U	NS	***	NS	***	***	***	*	NS		5.9564	11.1878	14.7328
	Sand	B	***	***	***	NS	*	NS	***	***	***		3.4984	6.4848
		D	***	***	***	***	NS	**	***	***	***	**		4.6364
		U	***	***	***	***	***	***	***	***	***	***	***	
		mean	98.6	124.4	99.4	62.4	53.0	57.4	103.4	90.0	90.4	62.4	49.0	38.8

Table 4. Comparison of burrowing and anchoring drag in sculptured and smoothed shells of *Amblema plicata* in sand and sand/gravel mixture. Explanation as in Table 1.

			Sculptured						Smoothed					
			Sand & gravel			Sand			Sand & gravel			Sand		
			B	D	U	B	D	U	B	D	U	B	D	U
Sculpt	Sand & gravel	B		-4.8013	-3.4066	11.2374	6.5217	7.4128	-1.0337	-1.4892	0.5995	12.1166	10.2793	12.9917
		D	***		1.1543	18.4661	12.5064	13.6283	2.9745	3.8811	4.6474	18.7966	16.1207	20.2540
		U	**	NS		15.2313	10.2549	11.2061	1.8969	2.3516	3.5005	15.8558	13.7628	16.8974
	Sand	B	***	***	***		-5.0874	-4.2693	-10.0322	-15.9706	-8.0651	2.4992	1.0232	3.1478
		D	***	***	***	***		0.8985	-6.4640	-9.4366	-4.6481	6.5766	4.0394	7.4066
		U	***	***	***	***	NS		-7.1605	-10.6248	-5.3129	5.8889	4.1603	6.7195
Smooth	Sand & gravel	B	NS	**	NS	***	***	***		-0.1043	1.4451	10.9145	9.6301	11.4401
		D	NS	**	*	***	***	***	NS		1.8716	16.3724	13.5179	18.0156
		U	NS	***	*	***	***	***	NS	NS		9.0292	7.8656	9.4808
	Sand	B	***	***	***	*	***	***	***	***	***		-0.9326	0.2039
		D	***	***	***	NS	***	***	***	***	***	NS		1.1767
		U	***	***	***	**	***	***	***	***	***	NS	NS	
		mean	79.1	95.4	91.4	48.2	59.0	56.8	83.4	83.8	76.7	43.4	45.8	43.0

The angles of the medial anchor and U2-D2 arms are grouped in Fig. 4. Both groups have a single well-defined mode and a narrow range of actual values. The medial anchor has a mean of 77.8° with a standard deviation of 4.9. The U2-D2 anchor has a mean of 35.4° and standard deviation of 2.7.

The values of *k* derived from the allometric equation fit to sculptural intervals show that all species examined possess allometric densing (Fig. 5). Values ranged from 0.23 to 0.50, all well below the isometric value of 1.0. The interval between ribs or knobs in medial anchors or U2-D2 arms is smaller than would be expected by isometric growth.

The results of the anti-scouring experiment are shown in Fig. 6. Like the results of Stanley (1981), these are strictly qualitative. It is apparent that the smoothed side was excavated to a greater extent, with more sediment removed revealing more shell than with the unaltered side in both species, even though not all sculpture could be eliminated from the shell of *Tritogonia verrucosa.*

DISCUSSION

ADAPTATIONS TO SOFT SUBSTRATA

Perhaps the foremost danger to an organism living in or on a soft substratum is sinking (Eagar, 1950). This liability may preclude invasion by large predators and equal-sized competitors, which would sink just as readily. The underlying consideration of a functional model or paradigm for shell form and sculpture for this type of bivalve is fairly unambiguous: increase buoyancy. This may be attained by two means, both of which occur in the freshwater bivalves: increase aspect to substratum and reduce shell weight. This discussion is limited to hypothetical considerations of the paradigm, and does not have the weight of experimental evidence found in other parts of this study.

Lea (1829) recognized that some unionoideans possessed a structure in which the shell extends dorsally above the hinge posterior and anterior to the umbo, uniting the left and right valves in an uninterrupted fold. He referred to these as symphynote shells. To separate the valves completely, the shell must be broken along this structure, which

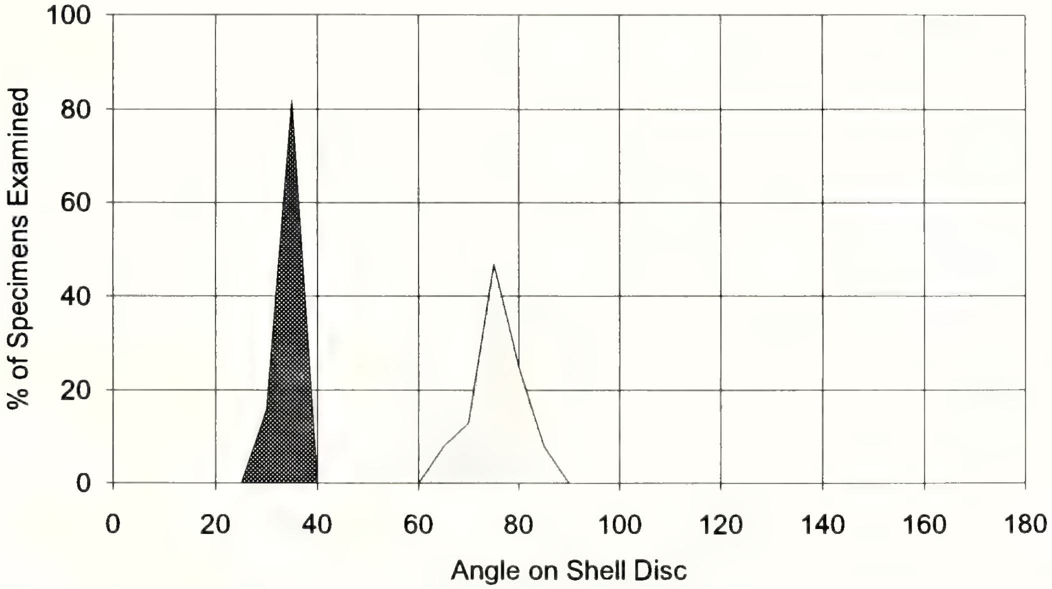


Fig. 4. Distribution of U2-D2 arm angles (dark shading) and medial anchor angles (light shading) in 5° increments over disc of shell.

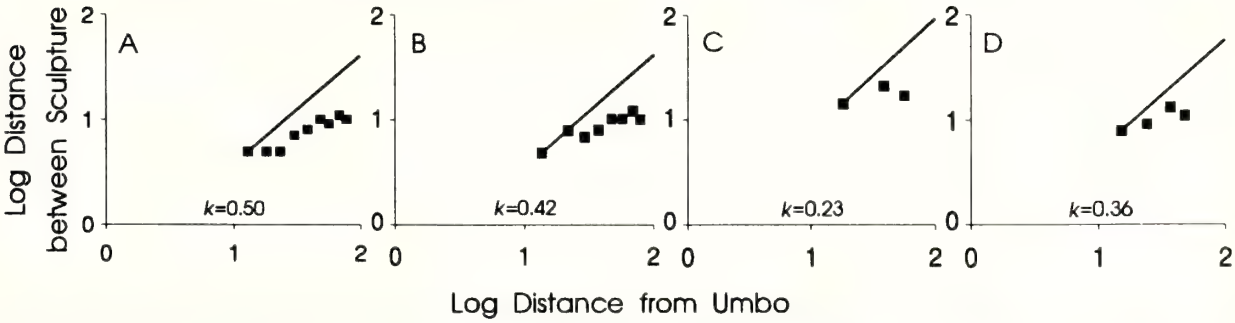


Fig. 5. Allometric plots of distance between sculpture (medial anchor or U2-D2 arms) and distance from umbo. ■ , observed values. Diagonal line - expected isometric line (k = 1.0). k, allometric coefficient for observed values. (**A,** *Amblema neisleri*; **B,** *Plethobasus cicatricosus*; **C,** *Obliquaria reflexa;* **D,** *Plectomerus dombeyana).*

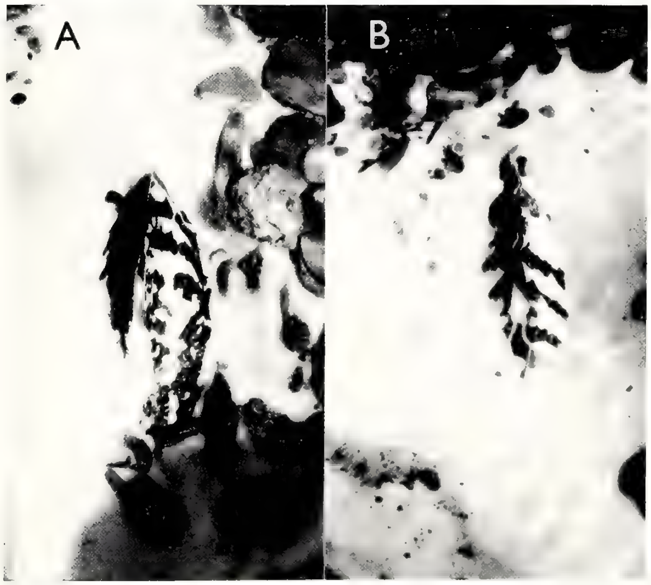


Fig. 6. Effects of anti-scouring sculpture (left valve) and smoothed (right valve) in sand. **A,** *Quadrula quadrula*; **B,** *Tritogonia verrucosa*. Direction of current is from top to bottom. Shell is oriented with umbo at bottom.

encases the functional ligament. This structure has arisen independently in many genera: the unionids *Lasmigona, Leptodea, Potamilus*, some *Anodonta,* and others; and in the hyriids, *e.g. Prisodon, Paxyodon*, and *Triplodon* (Fig. 7).

Symphynote species are rare in Recent marine groups, occurring most often in the Pinnidae, Pteriidae, and Mytilidae. In both the Pinnidae and Mytilidae, the symphynote condition appears to act as a secondary hinge in these essentially teeth-less groups. Members of the Pteriidae are largely byssate, epifaunal species, often occurring in areas of significant wave action. The symphynote "wings" or alae have been shown to act as rudders that enable the bivalve to pivot along its byssus and maintain a minimum aspect into the current (Stanley, 1972).

Most symphynote unionoideans are large, unsculptured, thin-shelled, and complanate. These are the same characteristics that Thayer (1975) predicted for bivalves in soft substrata in general. The habitat of these freshwater bivalves is often fine sand or mud, with or without a current. A compressed shell offers less resistance to a current than an inflated one of similar volume in some orientations. It will lie flat on the substratum as the animal reburrows, being held down by the overlying current (pers. obs., Fig. 8).

A complanate shape also will act as "snowshoes" on soft substratum. This form is rare in marine groups. The contemporary marine *Corculum,* a cardiid, has the valves expanded laterally to rest on the substratum surface, although this may be an adaptation for maximizing light to its symbiotic algal colonies (Kawaguti, 1950). The Permian alatoconchids, also laterally expanded, appear to have among the most extreme "snowshoe" form of any bivalve (Yancey and Boyd, 1983). In contrast, the complanateness in unionoideans is a result of peripheral (gnomonic) expansion of the valves rather than lateral expansion.

Although the alae could also function somewhat as "secondary ligaments" (Owen, 1958; Savazzi and Peiyi, 1992) in unionoideans, many symphynote species possess a fully developed true ligament. However, many symphynote species also have reduced dentition. In these groups, the alae also function as hinge teeth by aligning the valves during closure and preventing shearing in those forms lacking well-developed dentition. These species often are found in soft substrata where shearing is minimal. Thus, although the hinge no longer fulfills its usual functions (valve alignment and anti-shearing) in some unionoideans, that function has been exapted to varying degrees by the alae. The loss of dentition is characteristic of unionoideans living in soft sediments, as explained below.

Thus symphynote shells may function in two different ways: 1) as a stabilizing shape in a current preventing the animal from being washed away if dislodged, and to attain a favorable orientation when righted; and 2) as a buoyancy or "snowshoe" device in very soft substrata. The function of alae is here interpreted as a method of increasing the degree of complanateness, with little increase in actual volume, while also acting as functional replacements

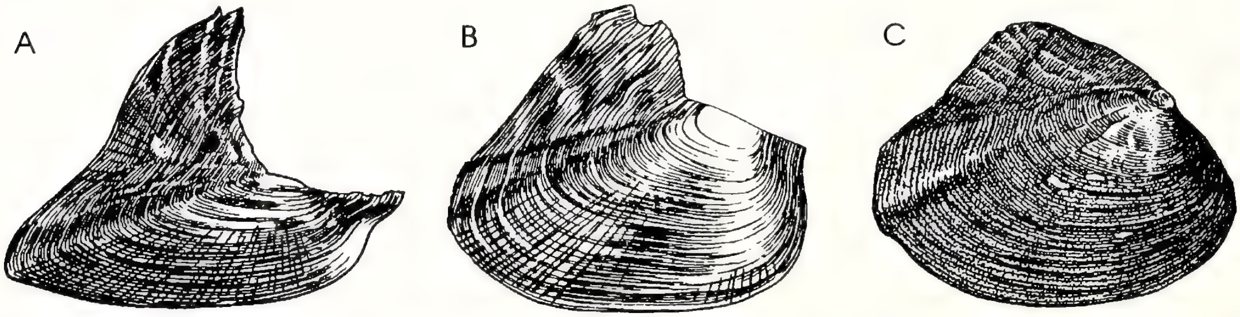


Fig. 7. Examples of Recent symphynote unionoideans. **A,** *Hyriopsis bialata* Simpson, 1900 (after Haas, 1969). **B,** *Cristaria plicata* (Leach, 1815) (after Clessin, 1873-1876); **C,** *Lasmigona complanata* (Barnes, 1823) (after Kuester, 1858-1859).

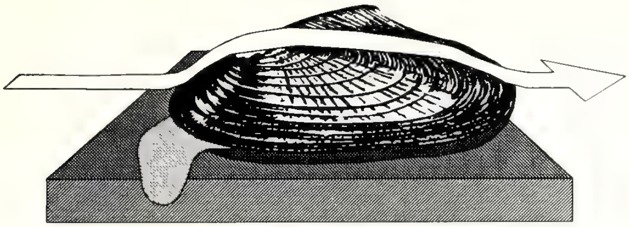


Fig. 8. Symphynote shape acting to hold shell to substratum during burial. Arrow, direction of water flow (shell modified after Kuester, 1858-1859).

for hinge teeth.

Reducing the density of the organism relative to the substratum is a straightforward problem. The weight of necessary organ systems scarcely can be diminished, but that of the shell, which is much denser than the soft parts, can be decreased significantly. The relative specific gravity of the whole animal is reduced in species having a thin shell (Eagar, 1977, 1978; Anderson and Ingham, 1978; Ghent *et al.*, 1978; Seed, 1980; Eagar *et al.*, 1984). Three avenues are available to lessen shell weight: decrease shell thickness; eliminate sculpture (heavy concentrations of shell material); or reduce or eliminate hinge teeth (also a major source of shell weight). Combinations of all three are found in soft-sediment unionoideans. Species of *Anodonta, Leptodea, Hyriopsis*, and *Potamilus* typically are thin-shelled, unsculptured, and have little or no dentition. These genera also are symphynote.

Increasing the aspect of the shell in a dorso-ventral plane to the substratum also will augment buoyancy by increasing the amount of shell surface normal to the substrate. Globose shells are more buoyant than non-globose ones in this orientation (Anderson and Ingham, 1978; Ghent *et al.*, 1978; Tevesz and McCall, 1979; Stern, 1983). When used together with thin shells, this can be an effective form in soft substrata, although such shells are susceptible to dislodgment by a current over that same substratum (Menard and Boucot, 1951). Few unionoideans have such a shell, among them: *Anodonta grandis s.l.* Say, 1829, *Potamilus capax* (Green, 1832), and some species of *Toxolasma* and *Lampsilis* (including the Miocene *Lampsilis marshalli* MacNeil, 1935). These species can be found in

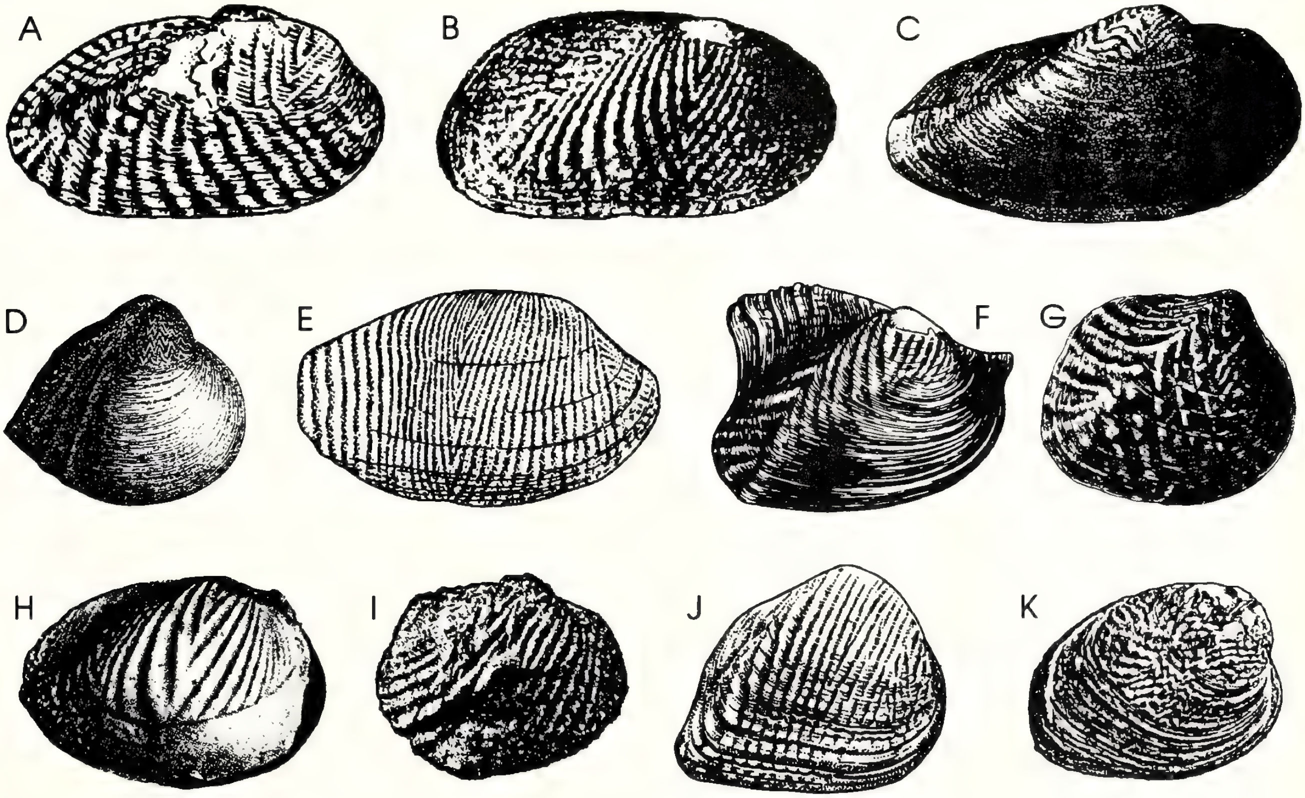


Fig. 9. Examples of divaricate sculpture in unionoideans. **A,** Recent *Scabies scobinatus* (Lea, 1856) (after Haas, 1969); **B,** Recent *Nodularia fluctigera* (Lea, 1859) (after Lea, 1860); **C,** Recent *N. douglasiae* (Gray, 1833) (after Lea, 1869); **D,** Cretaceous *"Unio" holmesianus* Dyer, 1930 (after White, 1907); **E,** Cretaceous *Nippononaia ryosekiana* (Suzuki, 1941) (after Suzuki, 1941); **F,** Recent *Triplodon rugosus* Spix, 1827 (after Haas, 1969); **G,** Recent *Quincuncina infucata* (Conrad, 1834) (after Burch, 1973); **H,** Oligocene *Diplodon latouri* (Pilsbry and Olsson, 1935) (after Párodiz, 1969); **I,** Cretaceous *Proparreysia letsoni* (Whitfield, 1907) (after Whitfield, 1907); **J,** Recent *Chevronaias colombiana* Olsson and Wurtz, 1951 (after Olsson and Wurtz, 1951); **K,** Recent *Parreysia houngdaranicus* (Tapparone-Canefri, 1889) (after Prashad, 1922).

muddy sand or silty environments in quiet water. Similar shell characteristics were found in marine bivalves that inhabit soft substrata (Nichols *et al.*, 1978).

The soft substratum modifications of the shell have evolved independently in many unionoidean lines, resulting in convergence of shell shapes. Many members of one group, the anodontine unionoids, have shell forms that seem especially evolved for this habitat. This group has anatomical and reproductive differences that set it apart from other unionoideans (Heard, 1975), a unique parasitic fauna (Vidrine and Bereza, 1977), and could represent an early offshoot of the Unionidae that exploited soft substrata.

ADAPTATIONS TO HARD SUBSTRATE

Divaricate Sculpture: Divaricate sculpture is surface ornamentation that forms a "V"-shaped pattern, often combining to form several continuous "V"'s (Fig. 9). This pattern is relatively easy to model mathematically, but considerably more complicated to explain biologically. Models for divaricate color patterns have been developed. North (1987) seemed to have given credit for the recognition and simulation of this pattern in the coloration of mollusc shells to Meinhardt and Klingler (1987), ignoring the earlier, very similar work of Waddington and Cowe (1969). Zimmer (1992) reported on the models of Fowler *et al.* (in press) which generated shell shape and color patterns in remarkable detail. Ermentrout *et al.* (1986) produced a model that also created color patterns similar to those found in mollusk shells. These models may be extended from the deposition of color to the deposition of shell material.

Although the area of sculpture may be concentric [or, more properly, gnomonic (see Stasek, 1963)], it cannot be deposited by the same accretionary process that forms concentric or radial ribs. Because the sculpture runs obliquely to the line of shell formation, the area of deposition must migrate laterally. To form "V-," or as is more common, "W"-shaped ridges, two additional conditions must be met: 1) the initial sculpture must originate at a single point and usually diverge; and 2) when two ridges converge, they end.

Nearly all unionoidean sculpture can be derived from a simple divaricate pattern. It seems likely that this pattern originated in the ancestral stock and has been exapted for new functions. The trigonioideans are considered by many workers to be the ancestors of freshwater bivalves (Morris, 1978). Tevesz (1975) and Newell and Boyd (1975) have pointed out the similarities between unionids and *Neotrigonia*: similar gill ciliary patterns, unfused mantle, prismato-nacreous shells, and filibranch gills. Stanley (1977a: 211) believed that the unionoideans were derived from "relatively unspecialized early representatives" of the trigonioideans.

Unionoidean sculpture can be derived from an ancestral divaricate pattern found in many trigonioideans, such as *Laevitrigonia, Quadratotrigonia, Litschovitrigonia*, and *Malagasitrigonia*, for example. Sculpture has been shown to be a conservative feature in trigonioideans (Stanley, 1977a), and other trigonioideans display the same derivations of the basic pattern as those found in the unionoideans. However, trigonioideans also possess sculpture that is very rare in unionoideans, although common in marine bivalves: concentric and radial ribs. Perhaps only the Triassic *Diplodon gregoryi* Reeside, 1927, and the Jurassic *Plicatounio* have true radial ribs, and no Recent unionoidean that I have seen has concentric sculpture [with the doubtful exception of the Recent *Lampsilis straminea straminea* (Conrad, 1834)]. Carter's comment that "*Castalia ambigua* [(Say, 1825)] [is] the only fresh water lamellibranch to possess radial ribs" (1968: 55) was incorrect. Other *Castalia*, also *Chevronaias*, have "radial ribs." However, these are not true radial ribs but divaricate ribs intersecting the shell margin at nearly right angles.

Several of the oldest unionoidean genera have distinctly divaricate sculpture. *Sulcatapex* from the Lower Cretaceous has divaricate beak sculpture and ribs on the dorsal slope. *Nippononaia,* also from the Lower Cretaceous, has pronounced divaricate sculpture, as does its potential descendant, *Trigonioides*. The Triassic *Diplodon haroldi* Reeside, 1927, is one of earliest to show this sculpture clearly. This type of sculpture thus has been evident in freshwater bivalves for at least 120 My.

For ease of explanation, a simple notation is used here to identify the parts of the prototype divaricate sculpture (Fig. 10). The apices of the pattern are numbered U1-U3 (U = up) from anterior to posterior. The apices point dorsally. The valleys of the pattern similarly are numbered D1-D3 (D = down). Thus the U's represent points of origination and potential bifurcation, while the D's are points where converging lines cancel out. A rib (or line of pustules) between two points is referred to as U1-D1, for example. Some species appear to possess more divarications than those found in the prototype, but the modifica-

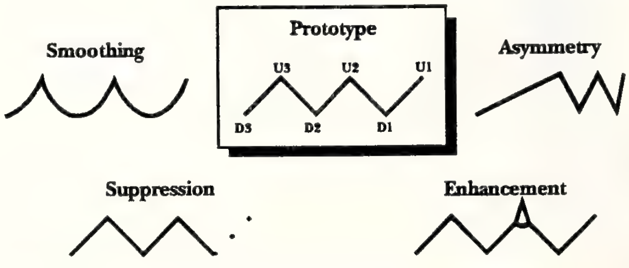


Fig. 10. Prototype divaricate sculpture and types of modifications.

tions essentially remain the same. The similarities between sculpture are geometric and do not necessarily represent phylogenetic paths. Similar sculpture may have arisen by convergence in unrelated groups.

Divaricate sculpture may be geometrically modified in unionoideans in four ways:

1) Asymmetry - all points of U and D may not be equidistant from each other, resulting in long and short U-D segments.

2) Suppression - prototype U-D segments may not be expressed. The U1-D1 arm often is absent. The U3-D3 arm usually is retained.

3) Enhancement - U or D points, rarely both, may be exaggerated into knobs or spines. The enhancement of points often accompanies suppression of arms.

4) Smoothing - the angular nature of the sculpture may become sinusoidal. This typically occurs at D points.

Divaricate sculpture in unionoideans often is divided into pustules, or combinations of ribs and pustules, and portions of the pattern may be suppressed. Erosion and injury can make the pattern unobservable. Sculpture also may be modified during ontogeny. It may become less pronounced, or completely disappear, during growth. Rarely, the sculptural pattern can change abruptly. This occurs most often with the metamorphosis from nepionic to adult or metaconch. These conditions have the result of obscuring the underlying divaricate pattern. However, most specimens clearly show divaricate sculpture.

In many species the apparent underlying pattern is modified by one or more of the means mentioned above. In *Amblema,* for example, the U2-D2 rib occupies most of the shell surface and may be the only remnant of the prototype pattern. *Obliquaria* usually retains only the U3-D3 arm as a series of ribs on the posterior slope (as do many species, see below), and the D2 point as an exaggerated knob. The unionids of the polyphyletic "genus" *Canthyria*, and juvenile *Unio pictorum* (Linné, 1758), have enhanced the D2 point into a spine. *Parreysia bhamoensis* (Theobald, 1873) also has juvenile spines (von Martens, 1899).

Seilacher (1973) found that some shell features seemed to constitute an array of burrowing sculpture, consisting of four features that readily can be observed:

1) Cross orientation - sculpture should be normal to burrowing for maximum friction. This includes divaricate sculpture that is only normal to movement at specific intervals during rotational burrowing.

2) Frictional asymmetry - the sculpture should present less friction in the direction of movement normal to it. This results in asymmetrical sculpture, also called "ratchet sculpture." Cross orientation usually accompanies frictional asymmetry to be functional as burrowing sculpture. Stanley (1969, 1970) observed that there were relatively few marine bivalves with this type of sculpture.

3) Perimeter smoothing - sculpture should be minimized at the area of maximum aspect (*i.e.* the shell disc) to minimize friction during burrowing. Seilacher's choice of the word "perimeter" potentially is misleading, as his perimeter is not the shell margin but the cross-section of the shell perpendicular to burrowing.

4) Allometric densing - sculpture size should remain the same magnitude throughout the growth of the shell. Typically, sculpture would be expected to increase in size proportional to shell growth. If the sculpture does not change size, then it is decreasing allometrically relative to shell size. The rate of sculptural growth is less than the rate of overall shell growth. This results in sculpture of approximately the same magnitude in juveniles as in large adults. This is thought to be an optimizing modification where the sculpture is most efficient against a particular sediment grain size at a particular sculpture size and spacing. Since the sediment particles do not increase in size as the bivalve grows, it would be advantageous to maintain sculpture at an optimum size, hence the allometric change in sculpture size relative to overall size increase. Allometric densing rarely is perfect as growth aspects typically can be observed.

Most unionoidean sculpture does not fit all four of Seilacher's criteria. Divaricate sculpture often is not oriented with burrowing, eliminating feature 1 of the paradigm. Although divaricate sculpture in some marine groups has been shown to enhance burrowing (Raup, 1969; Stanley, 1969, 1970), in unionoideans that particular orientation is unknown or the magnitude of the sculpture apparently is ineffectual. Frictional asymmetry (feature 2) is common in unionoideans, but is not oriented with burrowing. Furthermore, it is often oriented in opposite directions in different populations and as often the same sculpture may be symmetrical in others. Savazzi (1982) found that some marine species without frictional asymmetry can still have burrowing sculptures, but noted that those species do not burrow by the same method of most marine (or freshwater) forms. The third feature, perimeter smoothing, is replaced by "perimeter roughing" in most unionoideans, where the cross-sectional aspect is often the most highly sculptured region of the shell. Absence of sculpture on the anterior portion of the shell in otherwise sculptured species (anterior smoothing) also is not predicted by this model. Only the criterion of allometric densing (feature 4) is met in any degree in unionoideans (Fig. 5). In adult specimens of many species, the pustules and ribs are of fairly uniform size and interval across the shell (*e.g. Amblema, Megalonaias,* and *Plectomerus*). This is not unexpected if allometric densing optimizes sculpture for a particular sediment particle size, for whatever function.

Based on Seilacher's criteria for burrowing sculpture, unionoidean sculpture does not fulfill the conditions. Unlike marine species, burrowing sculpture is not common in unionoideans. It is proposed here that the functions of this sculpture are composite, with some parts acting as anchoring devices during and after burrowing against excavation by currents, and other parts as anti-scouring devices. Savazzi and Peiyi (1992) also reached this conclusion.

The Medial Anchor: A recurring theme in unionoidean sculpture is the medial anchor, a radiating area of sculpture across the medial disc of the shell. It can be the only sculpture on the shell or be part of a suite of composite structures (Figs. 11, 12). The anchor may be a series of pronounced knobs or spines. Often populations of taxa normally having a generalized anchor (see below) will have all sculpture absent *except* that forming the medial anchor. This sculpture is interpreted as an anchoring device during and after burial by a unionoidean against excavation by water currents. The sculpture can be substratum specific given the presence of allometric densing. The broad ribs of *Amblema, Megalonaias, Arcidens,* and others, also function as anchors, but differ in their derivation from the hypothesized prototype pattern, and will be discussed separately.

This structure is widespread in several unrelated genera, and may occur in only a few species in a genus. Examples of unionids with medial anchors include: *Obliquaria reflexa, Plethobasus cyphyus, Epioblasma torulosa torulosa,* and *Quadrula nodulata*. It reaches its most extreme development in the contemporary genus *Canthyria*, which may represent a polyphyletic group having convergent sculpture. Fossil species such as *Plethobasus aesopiformis*, and *Pl. biesopoides* Whitfield, 1907, *Proparreysia verrucosiformis* Russell, 1976, and *Pr. paucinodosa* also possess medial anchors. The prominent row of knobs on the Lower Cretaceous trigonoidean *Malagasitrigonia* resembles a medial anchor.

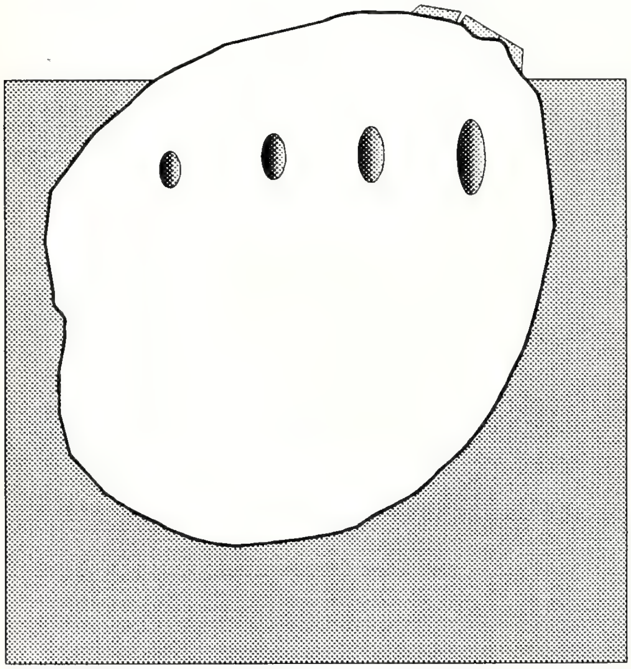


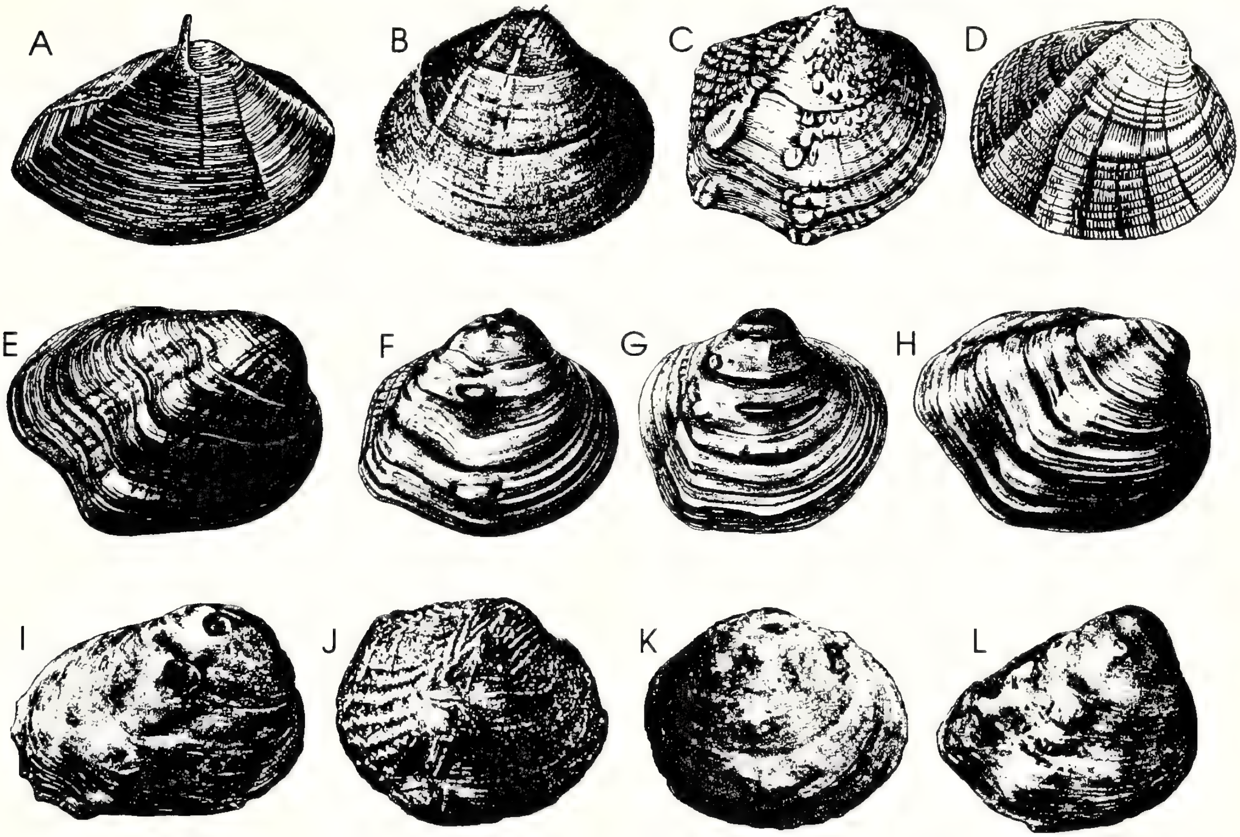
Fig. 11. Diagrammatic representation of a medial anchor.

The function of the medial anchor may be modeled and tested by a simple set of hypotheses: 1) the sculpture should be functional for its purpose; but 2) its corresponding detrimental effect on other functions must be minimized; 3) the anchoring device should be normal to the direction of potential excavation; and 4) for maximum effect, the sculpture should extend across the greatest area of the shell. Conditions 3 and 4 are structurally correlated in a bivalve shell because the normal axis of condition 3 is the approximate medial radius of growth. In elongated species, condition 4 may be compromised as the height becomes significantly less than the length, but these taxa rarely have a medial anchor. To meet condition 2, the sculpture should offer the least resistance in all attitudes other than the anchoring position. This is accomplished by elongating the sculpture perpendicular to the anchoring direction. Although this sculpture necessarily increases the drag of non-anchoring functions, its benefits apparently outweigh the increased friction.

We can construct an hypothesis to test this paradigm based upon conditions 1 and 2, and a separate one for condition 3 (4, as stated, may be unmet). If the sculpture acts as an anchor, it should create more drag than a non-sculptured species of similar size and weight, or the same shell with the sculpture removed. Furthermore, if condition 2 is to be met, the resistance should be less for orientations other than that of the anchoring attitude.

Comparisons of the amount of force (grams) needed to dislodge two unionid species with medial anchors are summarized in Tables 2 and 3. The anchors create drag in anchoring positions, with minimal drag along the direction of burrowing. The sculpture nevertheless produces substantial drag when compared with smoothed specimens. There is an indication that the sculpture may be optimized for the natural substratum and in the most common life orientation - with the umbo directed downstream.

Condition 3, that the anchoring sculpture should be normal to the direction of excavation, may be tested with two hypotheses. First, if sculpture does not have a function, there is no reason to suppose that sculpture should be concentrated on any one part of the shell disc more than on any other. If, however, sculpture occurs consistently in one sector and rarely elsewhere in many species, then a functional explanation for its position is suggested. Second, if sculp-



Fig, 12. Examples of the medial anchor in unionoideans. **A,** Recent *Canthyria spinosa* (Lea, 1836) (after Kuester, 1858-1859); **B,** Recent *Parreysia bhamoensis* (after von Martens, 1899); **C,** Recent *Quadrula quadrula* (after Lea, 1832); **D,** Recent *Dromus dromas* (Lea, 1834) (after Kuester, 1858-1859); **E,** Recent *Epioblasma torulosa torulosa* (Rafinesque, 1820); **F,** Recent *Obliquaria reflexa*; **G,** Recent *Q. nodulata* (Rafinesque, 1820); **H,** Recent *Plethobasus cyphyus* (Rafinesque, 1820) (E-H after Burch, 1973); **I,** Cretaceous *P. aesopiformis* (Whitfield, 1903) (after Russell, 1976); **J,** Cretaceous *Proparreysia letsoni* (after Whitfield, 1907); **K,** Cretaceous *P. paucinodosa* Russell, 1976; **L,** Cretaceous *P. biesopoides* (Whitfield, 1907) (K-L after Russell, 1976).

ture is found concentrated in one region, then to act as an anchor that region should be oriented to maximize drag in the direction of excavation.

The angle of the medial anchor sculpture (Fig. 4) was measured for 21 species. The results show a narrow range of anchor angles with only a single, well-defined peak, approximately normal to the shell length. In fact, the angle is closer to being normal to the actual angle of excavation because most unionoideans do not typically burrow at right angles into the substratum, but at an angle to it, resulting in the angle of excavation being slightly less than the predicted 90°. The observed offset of 12° may be a compensation for this effect.

The sector of the shell possessing the medial anchor corresponds to one of three points of the divaricate prototype sculpture: the U2, D1 or D2 point, and because of the accretionary growth process, the anchor will be a sector. This necessarily limits medial anchors to shells that are circular or nearly so. As elongation occurs, the U2 and D2 points are skewed posteriorly, removing them from their functional position. This is substantiated by the fact that no elongate species have medial anchors as adults.

Species having pronounced medial anchors typically are riverine species. Big river individuals of *Dromus dromas* have a medial anchor, while headwater specimens do not. The big river subspecies *Epioblasma torulosa torulosa* has a strong medial anchor, but it is weak in the headwater subspecies *E. t. rangiana* (Lea, 1839) and *E. t. gubernaculum* (Reeve, 1865). This feature, and others discussed below, form a suite of "Big River" morphological characteristics. Although it is easy to explain why these attributes are suited to big rivers, it is difficult to explain why they would not be beneficial in small rivers and creeks. These characteristics will be addressed in a later section.

The medial anchor is a refinement of existing sculpture (the generalized anchor, below) in response to a habitat characterized by a strong current. Sculpture such as the medial anchor may be retained despite suppression of other sculpture. In some groups, such as *Quadrula,* the medial anchor occurs along with other sculpture. In *Q. pustulosa,* the medial anchor can be present alone or be part of the generalized anchor. In *Q. nodulata*, the medial anchor is nearly the only sculpture expressed. In the Cretaceous *Proparreysia letsoni*, both divaricate sculpture and anchoring knobs are present.

The results suggest that poorly developed medial anchors are less effective than well-developed generalized anchors. The evolutionary shift from a generalized to an effective medial anchor cannot be made gradually without passing through a less efficient phase with decreased selective advantage (unless an additional, unidentified character is synergistic). Well-developed medial anchors such as those on *Obliquaria reflexa* could arise through major morphological shifts. This may explain the relative rarity and scattered occurrence among genera of this sculpture in the unionoideans, and why many of the taxa possessing it are found in either numerically small or monotypic genera. The medial anchor is best considered a more efficient refinement of the generalized anchor in which sculpture is retained on the shell disc only in its most functional position.

In some genera, such as *Amblema, Megalonaias, Arcidens,* a medial anchoring device has taken a form different from that found in *Obliquaria reflexa,* and is derived by a different method from the prototype sculpture (Fig. 13). In these groups, the U2-D2 arm has been extended across most of the shell disc (modification by asymmetry), occasionally with all other sculpture suppressed. In the latter case, the same arm acts as an anchor on the disc of the shell and an anti-scouring device on the posterior slope (anti-scouring sculpture is considered in a later section). The angle of the arm does not meet the paradigm for burrowing sculpture, but functions as an anchor, and is contingent on the geometry of the hypothetical prototype sculpture. To bring an arm into an anchoring position requires that the arm be greatly lengthened. Lengthening moves the U1-D1-U2 arms so far forward that they are eliminated by anterior smoothing. The D2-U3-D3 arms are moved so far posteriorly that the U2-D2 arm may usurp their function on the posterior slope as an anti-scouring device. As with the medial anchor, the angles of the U2-D2 arms for different species (Fig. 4) are very similar to each other (mean = 35.4°; SD = 2.7), suggesting a common function.

This U2-D2 sculpture fulfills the same function as the medial anchors, but has arisen by a different route. Clarke (1982) believed that the ridges aid in maintaining the effective orientation of the bivalve in the substratum. He did not state how he envisioned this anchoring function to occur, but proper orientation would be expected as the by-product of anchoring devices. In general, *Amblema*-like sculpture forms anchors by enhancing divaricate arms while *Obliquaria*-like sculpture forms anchors by enhancing divaricate points.

Clearly, not all riverine species possess such anchoring devices. It must be stressed that anchoring devices are but one evolutionary response to a riverine habitat and that other responses have occurred in other groups. Analogously, Seilacher (1973: 451) found sculptured and smooth marine bivalve forms living side by side in soft substrate. He concluded that "Why the one or the other strategy is chosen in a particular case, remains unknown, particularly since smooth and sculptured forms are found living side by side."

The Generalized Anchor: The least functionally specialized type of anchor is here interpreted as the most primi-

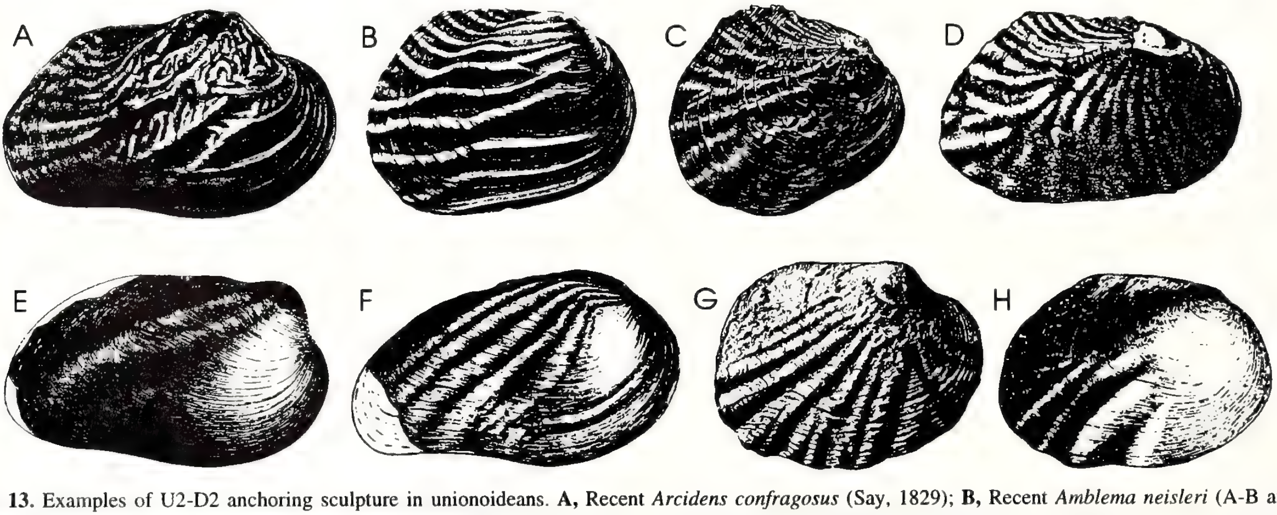


Fig. 13. Examples of U2-D2 anchoring sculpture in unionoideans. **A,** Recent *Arcidens confragosus* (Say, 1829); **B,** Recent *Amblema neisleri* (A-B after Burch, 1973); **C,** Recent *Megalonaias boykiniana* (Lea, 1840) (after Simpson, 1900); **D,** Recent *Elliptoideus sloatianus* (Lea, 1840) (after Lea, 1842); **E,** Cretaceous *"Margaritana" nebrascensis* White, 1883; **F,** Cretaceous *"Unio" belliplicatus* Meek, 1864 (E-F after White, 1907); **G,** Miocene *Megalonoidea rugicosta* MacNeil, 1935 (after MacNeil, 1935); **H,** Cretaceous *"Unio" gonionotus* White, 1883 (after White, 1907).

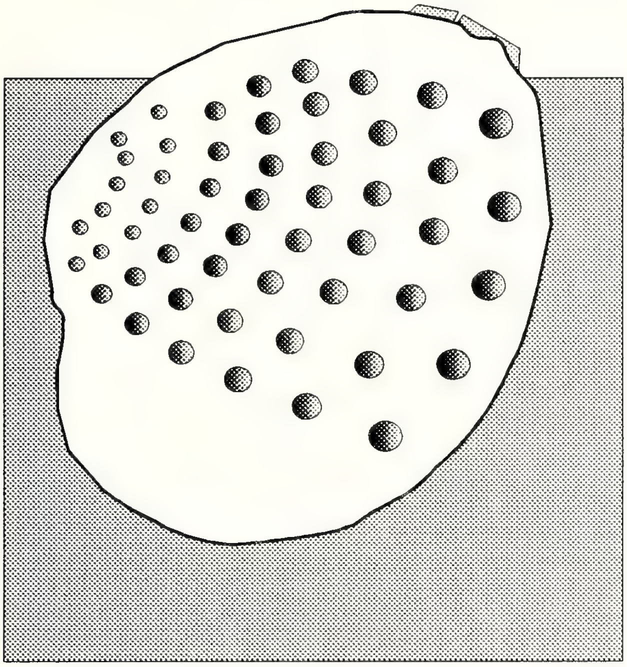


Fig. 14. Diagrammatic representation of a generalized anchor.

tive. It occurs in many unionoids (particularly the amblemines) and hyriids, in small groups of often unrelated genera. The generalized anchor is characterized by many pustules, or pustules coalesced into ribs, that are not confined to any specific area of the shell disc, but occur nevertheless in a divaricate pattern (Figs. 14, 15). The pustules and ribs are often symmetric individually, and therefore do not meet criteria 2 and 3 of the medial anchor paradigm. The sculpture acts as an anchor in most species, as suggested by Clarke (1982), but would hinder burrowing. It could be that in the absence of synergistic functional effects, the selective advantage of anchors (*i.e.* the ability to remain buried) is greater than the selective advantage of lacking sculpture (*i.e.* the ability to rebury efficiently) in many species. This type of anchor may be directional, the most efficient orientation being with the umbo downstream, the most prevalent position found in unionoideans in nature.

Fossil unionoideans often have a generalized anchor that displays the ancestral divaricate pattern with little alteration. Species such as *Proparreysia holmesiana, P. maclearni,* and *P. barnumi* (all Dyer, 1930), *Tritogonia natosini* (McLearn,1929) (see White, 1907; McLearn, 1945; Russell, 1967, 1976), and *Diplodon haroldi*, all are sculptured heavily with divaricate patterns. Several trigonioideans also have this sculpture, *e.g. Korobkovitrigonia, Steinmanella,* and *Litschkovitrigonia.*

Anti-Scouring Sculpture: In a water current, partially buried obstacles, whether they are stones or bivalves, tend to be excavated by scour. Water flowing near the water/sediment interface moves slower than water in overlying layers, causing a local vortex, which, when it contacts an

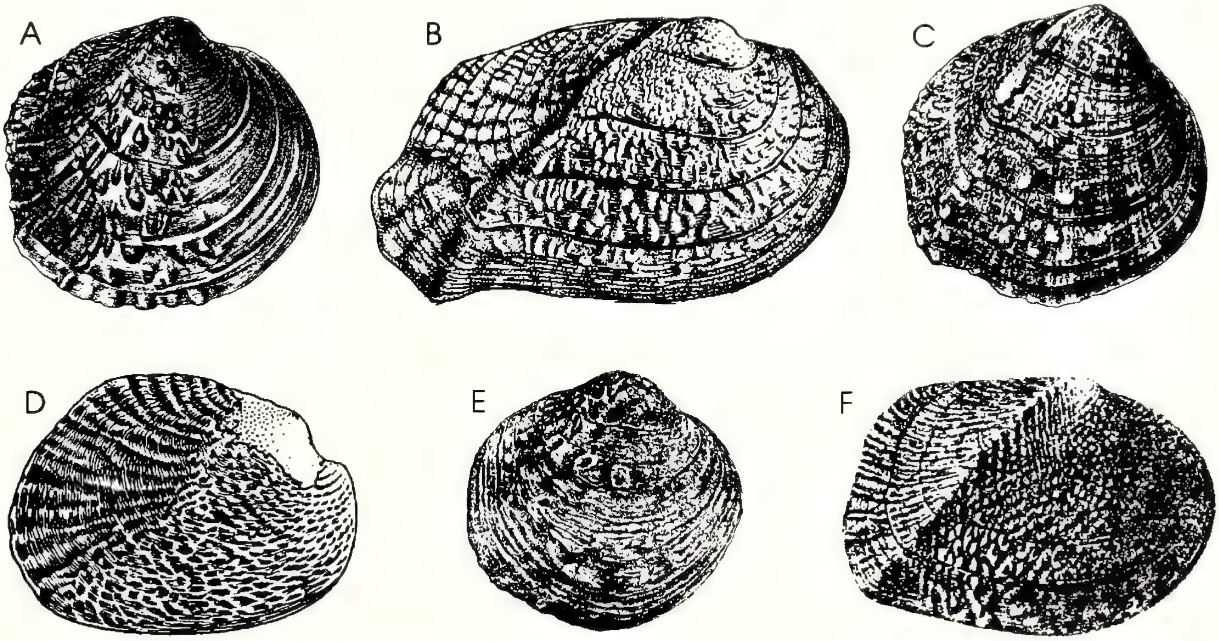


Fig. 15. Examples of the generalized anchor in unionoideans. **A,** Recent *Cyclonaias tuberculata* (after Burch, 1973); **B,** Recent *Tritogonia verrucosa* (after Kuester, 1858-1859); **C,** Recent *Cyprogenia stegaria* (Rafinesque, 1820) (after Burch, 1973); **D,** Recent *Discomya radulosa* (Drouët and Chaper, 1892) (after Haas, 1969); **E,** Cretaceous *"Unio" verrucosiformis* Whitfield, 1903 (after Whitfield, 1907); **F,** Recent *Quadrula apiculata speciosa* (Lea, 1862) (after Lea, 1863).

obstacle, will begin scouring the area around the barrier when a critical velocity is attained (Richardson, 1968). The resulting scour may destabilize the object to the point of dislodgment. Stanley recognized three different types of shell sculpture or form in marine bivalves that function to minimize scour. All three occur in unionoideans.

A common sculpture appearing in unionoideans is radiating ribs or corrugations on the dorsal slope (Figs. 16, 17). This feature occurs in a minority of species of otherwise unsculptured genera, such as *Elliptio, Lasmigona,* and *Ptychobranchus*, and is nearly always present in sculptured species. Even when the shell is devoid of this sculpture, sometimes, such as in several *Elliptio* species, the periostracum becomes ribbed in this region over the smooth shell. Dorsal ribbing is found first in Cretaceous unionids such as *Rhabdotophorus gracilis* Russell, 1935. White (1907) illustrated four: *Unio senectus, U. goniambonatus* White, 1878, *U. gonionotus,* and *U. aldrichi.*

Dorsal ribbing acts as an anti-scouring device by breaking the scouring vortex into random currents. Thus, although some currents remove sediment, others deposit them, so that the net result is no scour. The ribs are formed in nearly all cases by U3-D3 arms. In some species the U2-D2 arm extends to the dorsal margin, where they function in the same manner. Dorsal ribbing is often an adult sculpture, although sometimes becoming obsolete on large individuals. A maximum critical weight can be reached where anti-scouring sculpture is no longer needed. At the other extreme, nepionic shells are small enough that scouring is not a complication, the individuals being only slightly larger than some sediment particles. The main threat here is dislodgment by virtue of small size, and a premium is placed on anchoring devices, including byssal threads.

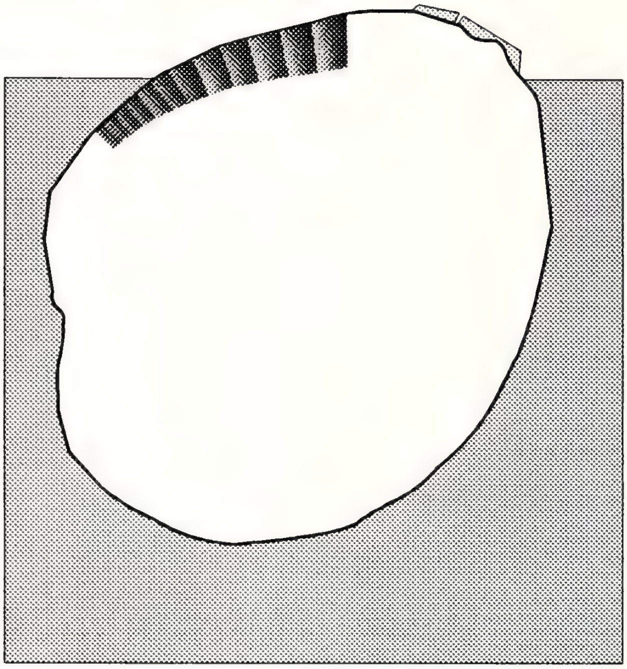


Fig. 16. Diagrammatic representation of anti-scouring sculpture.

Anti-scouring sculpture also can show allometric densing, where the magnitude of the sculpture does change isometrically during growth. This could be an optimization for a particular sediment size. Anti-scouring sculpture is most effective with small sediment particles. Although larg-

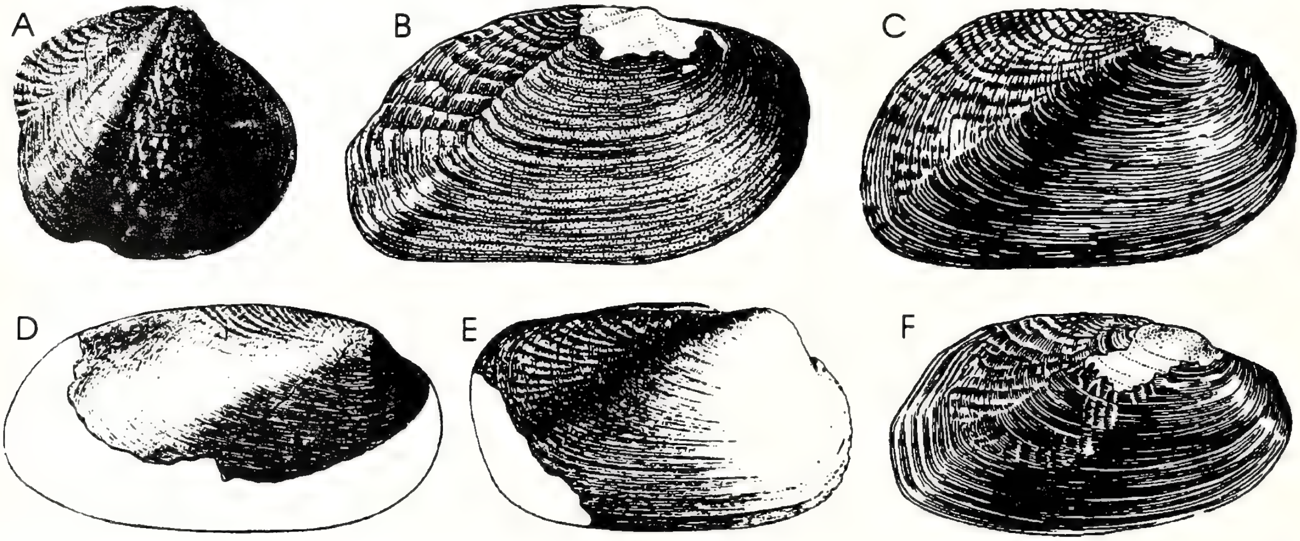


Fig. 17. Examples of anti-scouring sculpture in unionoideans. **A,** Recent *Quadrula rumphiana* (Lea, 1852) (after Lea, 1858); **B,** Recent *Lasmigona costata* (Rafinesque, 1820) (after Kuester, 1858-1859); **C,** Recent *Schepmania nieuwenhuisi* (Schepman, 1892) (after Haas, 1969); **D,** Cretaceous *"Unio" senectus* White, 1883; **E,** Cretaceous *"Unio" aldrichi* White, 1883 (D-E after White, 1907); **F,** Recent *Pseudodon loomisi* Simpson, 1900 (after Haas, 1969).

larger particles are less affected, the interstitial sand and silt renders the surrounding substratum more stable.

As ubiquitous as dorsal sculpture, is the presence of a dorsal ridge in unionoideans. Nevertheless, the dorsal ridge is uncommon in marine taxa. The function of both dorsal ribbing and the dorsal ridge in marine groups have been hypothesized by Stanley (1977b, 1981) as anti-scouring devices. The dorsal ridge coincides with the U3 point and often with the mantle area joining the inhalant and exhalant siphons. The dorsal ridge does not occur randomly, but at a point of divarication. Although a dorsal ridge is nearly ubiquitous in modern unionoideans, it seems absent in some species. The Triassic taxa *Unio felchii* White, 1883, and *U. toxonotus* White, 1883, appear to lack this feature, as do several species of Recent *Elliptio*. Thus, the dorsal ridge is not a necessary, structural consequence of valve morphometry, but an adaptive feature that has arisen in most living unionoideans.

An additional anti-scouring feature found in unionoideans is the dorsal slope itself. Although sculptureless, this type of shell-form was hypothesized by Stanley (1975b, 1977b) as an effective deterrent to scouring. The effect is not due to the ridge, but to the constriction of the shell posterior to it. The concave shape of the slope allows scouring currents to flow over it without excavation. This design is most effective in unstreamlined species, where the slope may approximate the sediment surface. Many unstreamlined taxa have pronounced dorsal ridges/slopes: species of *Quadrula, Fusconaia, Pleurobema,* etc.

Anti-scouring adaptations only are necessary in regions having a current. It is significant to note the lack of these devices in most lacustrine taxa such as *Anodonta*, where appreciable unidirectional currents may not occur. Although Stanley (1981) believed that anti-scouring sculpture would result in burial in severe currents, this does not appear to be the case in unionoideans, where riffle species often have dorsal ribs.

Umbonal Sculpture: In many taxa, particularly the amblemines, the adult sculpture is directly derived from this nepionic structure (Howard, 1914). More importantly, species unsculptured as adults often have distinct beak sculpture. This implies a function for beak sculpture that may be retained in adults or lost. If the juvenile sculpture persists, the derived adult sculpture is an anchoring device (*e.g. Quadrula*). In taxa where it is does not persist, the species are often either streamlined forms *(Elliptio)*, or soft substratum forms *(Anodonta)*.

There is some evidence that umbonal sculpture acts as anchors in nepionic shells. The beak sculpture is often very coarse relative to the small shell size. The sculpture is oriented as anchoring devices and does not include dorsal ribbing, and therefore does not function as an anti-scouring device. Beak sculpture may be optimized for particle size (particles may be large relative to nepionic shells, hence the coarse sculpture), and oriented to minimize dislodgment. The lack of anti-scouring devices is explained by the very small size of nepionic shells, which presumably would not create appreciable scour. At some critical weight or size, anti-scouring sculpture may become necessary.

Clarke (1986) and Yeager *et al.* (1993) have shown that some unionids may be buried after metamorphosis, and Clarke noted that species that lack umbonal sculpture usually were thick-shelled after transformation. He believed umbonal sculpture to be a predator deterrent. I disagree with this hypothesis, at least as the main function of umbonal sculpture, but I believe his observations lend support for an anchoring function. This would be useful to a buried juvenile unionoidean, and a thick (heavy) shell may be sufficient to prevent dislodgment without requiring anchors.

Beak sculpture, like that of adults, is divaricate. In fact, the two types of sculpture should not be considered distinct, but a continuum of sculpture that may change during ontogeny (Howard, 1914). Dall's (1895: 523) contention that "the sculpture of the tips of the umbones is probably due to the influence of the hooked or serrated edges of the glochidium valves" was incorrect. The geometry of the umbonal sculpture is independent of whether the glochidium possessed hooks or not. Three general patterns of beak sculpture are found: double-looped, single-looped, and barred. All are derived from the prototype sculpture. The single-looped and barred are here considered as a smoothed double-looped sculpture, rather than as a single, unsuppressed "V."

Big River Morphology: Some amblemines are known to exhibit a clinal change of form from headwaters to the most downstream reaches (Ortmann, 1920; Ball, 1922; Grier and Mueller, 1926; Goodrich and van der Schalie, 1944; Eagar, 1950; Clarke, 1973; Tevesz and Carter, 1980; Clarke, 1982; Stansbery, 1983). Ortmann referred to this as the Law of Stream Distribution. The downstream form of *Fusconaia flava,* for example, contains a full suite of features adapted to a riverine habitat, while headwater specimens are lacking these features (Fig. 18). Comparison of headwater and "Big River" morphs reveals that significant differences exist between the burrowing and anchoring capacity of *F. flava* (and presumably other taxa) in these two habitats. The headwater form offers less resistance to burrowing than the downstream form, but the latter is more efficient as an anchor. Downstream features in *F. flava* include high, prosogyrous umbones, a relatively thicker shell, a more globose shape, and a more defined sulcus. The same differences

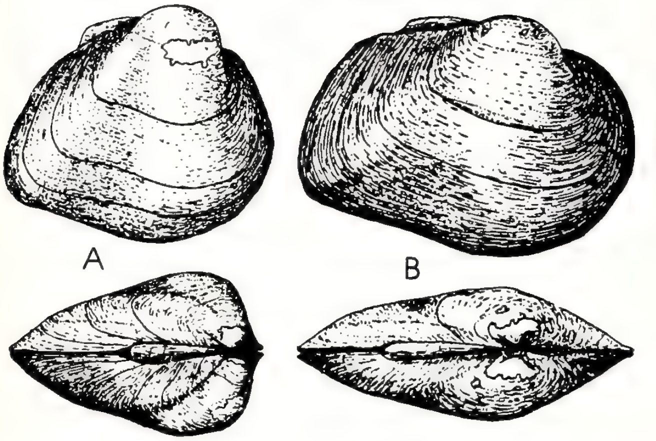


Fig. 18. Big River morphs of *Fusconaia flava* (after Call, 1898). **A,** Big River. **B,** Headwaters.

occur in other species, and the fact that unrelated forms show the same type of clinal variation suggests a common function. The convergence in shapes, and therefore clines, is a common reaction to similar environmental conditions in which the adaptive responses are limited by shell geometry and an intrinsic sculptural pattern.

Infaunal, free-living marine bivalves do not show "Big River" modifications, although Rosenburg (1972) found that a species of venerid was slightly more elongate in these tidal areas. The important consideration here is *constancy of current*. Open ocean populations may experience no net water movement. In riverine habitats, the direction of the current remains constant, but variable in degree, for perhaps tens of thousands of years or more. I suggest that marine groups have had little opportunity to evolve current-resistant shell forms and sculpture on a large scale, while in unionoideans this has been the paramount adaptation.

The downstream features are predictably strong current adaptations. Such changes are most prominent in sculptureless taxa. High umbones, increased shell thickness, and a strongly prosogyrous orientation move most of the mass of the shell to the anterior margin. Sculpture is reduced or absent, its function now filled by the prosogyrous umbones (Stanley, 1977b). The high prosogyrous umbones create a center of mass near the anterior margin on a broad lunule base (Fig. 18) (see also Savazzi and Peiyi, 1992). The post-umbonal region of the shell, often distinctly narrowed by a sulcus, now assumes a laterally flattened, conical, hydrofoil-shape conducive with hydrodynamically pushing the shell toward the substratum. Stanley, in his study of anti-scouring devices in trigoniids, stated that this paradigm was "usually associated with the prosogyre condition" (1977b: 883). Thus, downstream characteristics function to position the shell such that the anterior margin is directed toward the substratum, the optimum burrowing orientation. Stanley (1972) found a similar orienting function for this association of characteristics in marine byssate bivalves.

Taxa having "Big River" characteristics occurred at

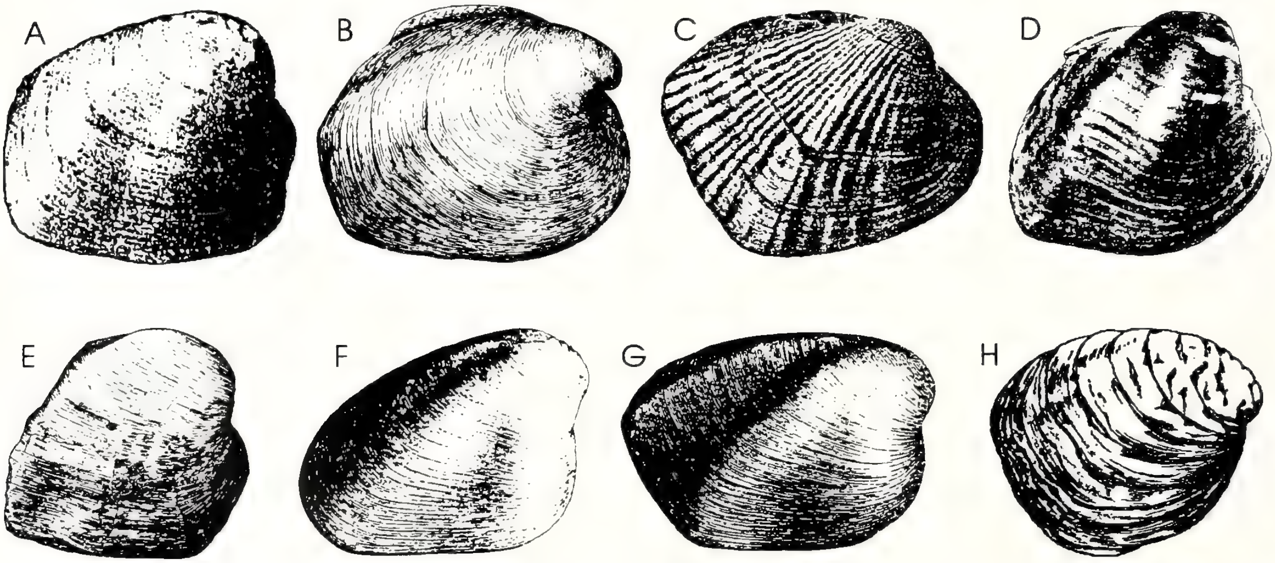


Fig. 19. Examples of Big River characteristics in unionoideans. **A,** Recent *Iheringella isocardioides* (Lea, 1856) (after Lea, 1857); **B,** Recent *Fusconaia ebena* (Lea, 1831) (after Call, 1898); **C,** Recent *Epioblasma sampsoni* (Lea, 1861) (after Lea, 1863); **D,** Recent *F. flava* (after Baker, 1898); **E,** Cretaceous *"Unio" dawsoni* Russell, 1931 (after Russell, 1931); **F,** Cretaceous *"Unio" propheticus* White, 1876 (after White, 1907); **G,** Cretaceous *"Unio" proavitus* White, 1883 (after White, 1907); **H,** Pliocene *Parunio crassus* Ping, 1931 (after Ping, 1931) .

least as far back as the Jurassic (Fig. 19). White (1907) illustrated several examples: *Unio stewardi* White, 1883, *U. endlichi* White, 1877, and *U. proavitus. U. stewardi, Vetulonaea faberi,* and *V. whitei* Branson, 1935, bear a strong resemblance to contemporary big river *Pleurobema,* and *U. proavitus* is virtually identical with big river *Epioblasma*, such as *E. sampsoni*. Others, such as *U. dawsoni*, have no Recent counterparts.

As headwater individuals may occur in water with currents equally as strong as downstream ones, it is difficult to explain why upstream populations lack these riverine devices. The shape of some unionoideans approaches in magnitude the most streamlined forms found in marine taxa, but is not related to tube-dwelling or active burrowing beneath the substratum (Watters, 1992). Eagar (1978) and others have suggested that it is the occasional unusually strong currents (*i.e.* floods) in headwaters that have selected for streamlined forms.

DISTRIBUTION OF UNSCULPTURED UNIONOIDEANS. The presence of sculptured species co-occurring with unsculptured ones is difficult to explain. The distribution of sculpture by river size clearly shows that sculptured taxa tend to occur in big rivers, while unsculptured taxa live in a wider range of river sizes, although mostly found in small systems. Headwater individuals tend to have less anchoring and anti-scouring sculpture than do big water forms, and Lewis and Riebel (1984) showed that unsculptured unionids were able to successfully burrow in a variety of substrata, including clay, sand, and gravel. It is likely that most unionoidean speciation has taken place in the isolated headwaters of rivers during periods of marine transgressions. This is particularly true of southern and eastern unionoidean species, which have experienced a much greater degree of transgression-related isolation than interior basin systems (Johnson, 1970, 1972; Sepkoski and Rex, 1974; Butler, 1990). There is evidence that at least the members of the genus *Elliptio* have speciated at a high rate in these areas relative to the interior basin. Three species occur in the interior basin, but perhaps as many as 31 live in coastal rivers. The largest number of endemic species of unionids occurs in coastal rivers. Most important, except for the three species of the east coast endemic "genus" *Canthyria,* no east coast species has any pronounced sculpture. The Coastal Plain has no representatives of the typically big river, interior basin, sculptured genera such as *Amblema* or *Megalonaias*. The most diverse of the sculptured unionoidean genera, *Quadrula*, has no east coast representatives, reflecting the fact that no large river bisects the Appalachian Divide (except the New River, but that river is interrupted by high falls), and that members of this big river genus did not have the chance to establish themselves in the headwaters of eastern rivers. However, the Coastal Plain has many representatives of interior headwater genera: *e.g. Elliptio, Lampsilis,* and *Villosa*.

This represents circumstantial but compelling evidence that east coast species may be derived primarily from central interior headwater taxa by sharing of habitat or host fishes in the headwaters. Because headwater taxa generally are sculptureless, the derived taxa on the east coast also are sculptureless. Gulf drainage species have sculptured representatives, but these are generally associated with large interior rivers (Apalachicola River, Alabama River, etc.) or rivers close to the Mississippi River drainage (*e.g.* Pearl River) from which taxa could have spread through stream capture or lowland exchange of host fishes between ancient big river confluences.

This study suggests that shell form and sculpture could be selectively advantageous for different substrata and habitats. However, whether unionoideans actively select a particular substratum is not understood. Tevesz and McCall (1979) and Bailey (1989) showed that one species apparently may move to a preferred substratum, but evidence for other species is not available. Many species often are found in a particular substratum, suggesting habitat preferences by them or their host (Harman, 1972; Sickel, 1980). But other studies have not supported this hypothesis (Horn and Porter, 1981), or have found mixed results (Huehner, 1987). Although Tadic (1960) and Tudorancea (1972) reported that unionoideans migrate, other authors suggested that they do not (Isely, 1911, 1914; Young and Williams, 1983). A species of the sculptureless genus *Lampsilis* has been shown to alter its shell dimensions when reciprocally transplanted between mud and sand to match that of the original population morphology (Hinch *et al.*, 1986), although growth rates seemed controlled genetically (Hinch and Green, 1989). The shell shape of *Elliptio complanata* (Lightfoot, 1786) was found to be narrower in coarse sand in deep water than in shallow water (Hinch *et al.,* 1989), and the degree of obesity was shown to increase in areas of high productivity (Podemski and Green, 1993) for *L. radiata* (Gmelin, 1781). Whether different habitats change the amount of sculpture has not been determined.

The genetic ability to construct sculptured shells may be lost in many unionoidean lineages, particularly those resulting from speciation in headwaters. The presence or absence of sculpture also may be tied synergistically to a more complicated suit of genetic effects. Both hypotheses are potentially correct, but they have not been explored in this study. The present co-occurrence of sculptured and unsculptured shells in medium sized rivers may indicate that headwater lineages have reinvaded the larger river reaches. Being sculptureless, extant species have adapted other shell-morphology characteristics to this habitat. The most commonly encountered adaptation is the "Big River Effect."

SUMMARY

The highly diverse sculpture found in the Unionoidea could be derived from ancestral trigoniids. In that group the main function of sculpture was as an aid to burrowing, but the sculpture of the unionoideans has been exapted for use as anchoring devices, although still superficially similar. The sculpture forms three types of anchors. The generalized anchor is considered the most primitive. The medial anchor is derived from the selective elimination of some generalized anchor sculpture and the selective enhancment of others. A third anchor is derived from the enhancment of a prototypical divaricate arm, often at the expense of most other sculpture. All anchors function to prevent dislodgement during and after burial, and to maintain a certain position in the substratum. Sculpture may be optimized for a particular substratum and life orientation.

The shells of many unionoideans also have antiscouring devices that tend to eliminate removal of substratum by currents adjacent to the shell. These devices also are found in ancestral trigoniids and include fluted posterior slopes, dorsal ridges, and concave dorsal slopes. They function mainly by retaining sand and silt that result in a more stable adjacent substratum.

Unionoideans living in soft substrata have modified the shell by several methods to increase buoyancy. These shells typically are thin, alate, and complanate, with a reduced or absent hinge. All of these factors decrease the relative weight of the animal in the substratum. These shells also function as "snowshoes" on soft sediments, and tend to hold the animal in place if dislodged in a current. A few species have achieved buoyancy by having greatly inflated shells, offering a greater aspect to the substratum. These shells however are unstable in a current.

The ability to remain buried through anchors, antiscouring sculpture, and ponderous, prosogyrous shells was central to speciation in large rivers, where presumably the earliest unionoideans invaded freshwater. But in the headwaters, a premium was placed on the ability to rebury if dislodged by floods. Apparently even anchors do not suffice in these conditions. Headwater taxa therefore generally have unsculptured, often streamlined, shells. The gradient of headwater forms to big river ones, the Big River Effect, is the result of these differing adaptations.

The greatest force operating on a unionoidean shell to drive morphological changes is the constancy of a unidirectional water current, a factor that did not shape the shells and sculpture of unionoidean ancestors. But the move to freshwater rivers necessitated the exaptation of pre-existing sculpture for unique, new problems encountered in riverine habitats.

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Freshwater mussels (Bivalvia: Unionidae) of the Hiwassee River in east Tennessee

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Abstract. Thirteen native species of freshwater mussels are reported from a 20 km stretch of the Hiwassee River, Polk County, Tennessee. *Fusconaia barnesiana* (Lea, 1838), *Elliptio dilatata* (Rafinesque, 1820), *Villosa iris* (Lea, 1829), and *V. trabalis* (Conrad, 1834) are the most abundant species present; the last taxon is included on the United States federal list of Endangered and Threatened Wildlife and Plants. *Epioblasma florentina walkeri* (Wilson and Clark, 1914), also included on the federal list and previously unreported from the Hiwassee River, is present but rare. This section of the Hiwassee is unaffected by a power generating dam and appears free of pollutants, thus serving as a refugium for viable populations of several mussel taxa. Inference is made to late prehistoric-early historic Hiwassee River mussel assemblages based on shell samples from aboriginal sites.

An approximately 20 km stretch of the Hiwassee River (HR), HR km 85.6-105.6, Polk County, Tennessee, flowing between the Apalachia Dam and the Apalachia Powerhouse, is unique compared with all other Tennessee Valley Authority (TVA) dams and river impoundment systems. The dam, built by the TVA and completed in 1943, is located in Cherokee County, North Carolina, 0.25 km from the Tennessee-North Carolina border. Maximum height of the dam is 45 m, its length 392 m; the lake (Apalachia Lake) is 16 km in length and its area at full pool is 440 ha. Rather than hydroelectric power being generated by turbines in the dam, the Hiwassee River (lake water behind the dam) is diverted through a tunnel hewn from rock and connected with sections of welded steel pipe 5.4 m in diameter. This conduit extends along the top of the bluff to the Apalachia Powerhouse 20 km downstream. Electric power is generated as reservoir water is released through paired pipes that descend vertically from the bluff to the Powerhouse directly below at the river's edge.

Downstream from Apalachia Dam is a gravel road that parallels the dam; during normal water levels a shallow pool of water forms between the road and base of the dam. Renewed flow of the Hiwassee River between Apalachia Dam and Powerhouse is maintained by a series of small- to medium-sized tributaries including Coker, Loss, Turtletown, and Wolf creeks and numerous smaller branches. Depth throughout this 20 km stretch of river, situated in a high gradient gorge of the Blue Ridge physiographic province, seldom exceeds 1 m, and then in only isolated pools. Substrata consist generally of large boulders, cobbles and gravel interspersed with areas of sand and occasionally fine silt. Uplifted ridges of exposed Precambrian sandstones divert the main channel into numerous side channels, and in some stretches this has resulted in marsh-like conditions supporting a variety of herbaceous species along banks and on small islands. Eastern hemlock [*Tsuga canadensis* (L.) Carr.], American sycamore (*Platanus occidentalis* L.), hornbeam (*Carpinus caroliniana* Walter), and rhododendron (*Rhododendron maximum* L.) are common in the flood plain and on the base of the bluffs, while common alder [*Alnus serrulata* (Aiton) Willd.] and water willow [*Justicia americana* (L.) Vahl.] abound on low islands and gravel beaches. Fishes typical of an upper Tennessee River warm-water habitat are found here. Several representative taxa occurring in the Hiwassee River between the Apalachia Dam and Apalachia Powerhouse are indicative of quality river habitat (Hitch and Etnier, 1974). These include cyprinid shiners [*Cyprinella galactura* (Cope, 1868), *Notropis leuciodus* (Cope, 1868), and *N. spectrunculus* (Cope, 1868)], centrarchids [*Lepomis auritus* (Linné, 1758), *L. cyanellus* Rafinesque, 1819, and *Micropterus dolomieui* Lacepede, 1802] and darters [*Etheostoma blenniodes* Rafinesque, 1819, *E. simoterum* (Cope, 1868), *Percina caprodes* (Rafinesque, 1818) and *P. aurantiaca* (Cope, 1868)].

At the lower end of this 20 km stretch at HR km 85.6, the Apalachia Powerhouse discharges a tremendous volume of cold reservoir water into the warm waters of the river. Substratum is scoured and temperatures are lowered. There is an abrupt change in physical parameters of the water and habitat below this point. The lower Hiwassee River becomes impounded by the backwaters of Chickamauga Reservoir (Tennessee River) at approximately HR km 41.6 before it enters its historic confluence with the Tennessee River.

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METHODS

Approximately 100 work-hours were spent collecting mussels in the Hiwassee River (HR km 85.6-105.6) during July (15), August (5, 15, 21), September (3, 10) and October (10, 15), 1992. Two specimens of *Lampsilis ovata* were collected alive; all other live unionids found were replaced in the substratum. The majority of specimens representing the other 12 taxa reported here was comprised of shells discarded by muskrats [*Odontra zibethica* (Linné, 1766)] following predation. Shells were left at feeding stations along the banks and on rock islands. Seven river km were surveyed for unionids, but, because of especially suitable habitat judging by the great abundance of shell at HR km 85.6 and 98.8, most of the collecting time was spent at these two locations. In addition, collections were made in Coker, Spring, Conasauga, and Chestuee creeks, the largest tributaries of the Hiwassee River in Polk County, Tennessee. All archaeological shell discussed in this paper and the majority of specimens collected during this study are housed in the Frank H. McClung Museum. Voucher specimens have been deposited in the Illinois Natural History Survey, Champaign-Urbana, the Illinois State Museum, Springfield, and the Carnegie Museum, Pittsburgh, Pennsylvania. Unionid taxonomy used in this study is from Turgeon *et al.* (1988).

RESULTS

Thirteen species were recovered during this study (Table 1). Numerous stretches of this braided 20-km section of the river were searched, but most lacked a stable substratum of fine gravel and sand; moderate to swift current flowing over bedrock prevented the establishment of suitable substrate for mussel populations. Although one locality, HR km 91.7-92.5, appeared to provide especially suitable habitat, only 22 specimens were found. Two other localities, however, HR km 85.6-86.4 (immediately upstream from the Powerhouse) and HR km 98.8, contained abundant mussel populations; 1201 and 1401 specimens, respectively, were obtained during approximately 40 work-hours of collecting at each locale (Table 2) during July-October 1992.

Differences between the size of populations of several species making up the mussel assemblage at these two localities are striking. Shells of *Villosa iris* comprised 82% of all specimens collected at HR km 98.8 (Fig. 1), while < 2% of the specimens collected at HR km 85.6 were *V. iris*. Nearly 25% of the mussels found at HR km 85.6 (Fig. 2) were *V. trabalis*, but at HR km 98.8 this species comprised < 2% of the population. At HR km 85.6, shells of *Fusconaia barnesiana* comprised 54% of all specimens collected, but only 7% at HR km 98.8.

Although differences in abundance of host fish for glochidia at these locations might affect mussel numbers, variations in habitat between these two sections of river are probably the determining factors. While both are characterized by a substratum composed of fine gravel, sand and silt, HR km 98.8 has an estimated mean depth of < 0.5 m with numerous channels divided by uplifted shelves of sandstone (Fig. 1). In contrast, HR km 85.6 has an estimated mean depth of 1.0 m; a few pockets in and near the main channel are 1.5-2.0 m deep. This is the widest section of river (Fig. 2), approximately 110 m, with some areas of little or no current.

Alasmidonta marginata, *Elliptio dilatata*, *Fusconaia barnesiana* and *Lampsilis fasciola* occurred at all localities with suitable habitat collected by us, but they var-

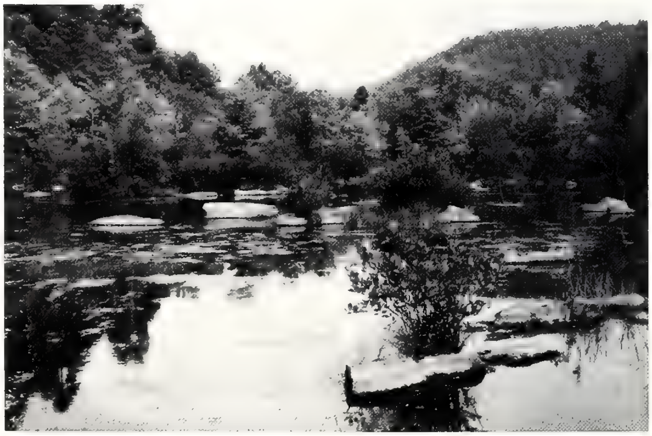

Fig. 1. Braided section of the Hiwassee River (HR km 98.8) ca. 3.5 km dowstream from the Apalachia Dam. Of the eight species identified from this locality, shells of *Villosa iris* (N = 1,153) comprised 82% of the sample.

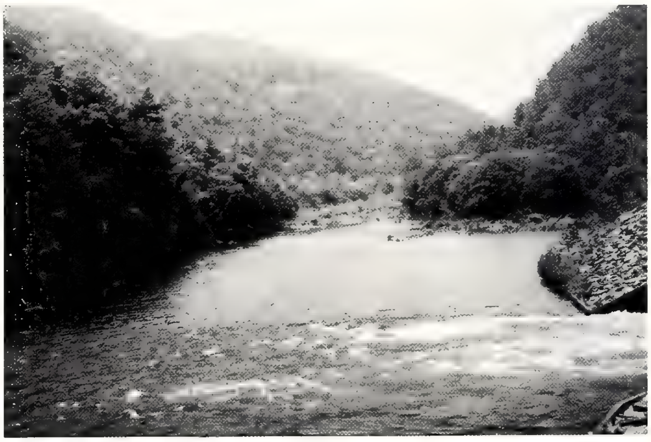

Fig. 2. Hiwassee River (HR km 85.6), looking upstream, where viable populations of *Villosa trabalis* occurred, and where 17 specimens of *Epioblasma florentina walkeri* were collected. Turbulent flow in foreground is discharge water from the Apalachia Powerhouse.

Table 1. Archaeological, pre-impoundment and 1992-1993 records of freshwater mussel taxa from the Hiwassee River, Polk County, Tennessee.

Species	Hiwassee Old Town	Ortmann (1918)	This study 1992-1993
Actinonaias ligamentina (Lamark, 1819), mucket	X		
Alasmidonta marginata Say, 1818, elktoe			X
Alasmidonta viridis (Rafinesque, 1820), slippershell mussel		X	
Amblema plicata (Say, 1817), threeridge	X		
Anodonta imbecillis Say, 1829, paper pondshell			X
Cyclonaias tuberculata (Rafinesque, 1820), purple wartyback	X		
Dromus dromas (Lea, 1834), dromedary pearlymussel	X		
Elliptio crassidens (Lamarck, 1819), elephant-ear	X		
Elliptio dilatata (Rafinesque, 1820), spike	X		X
Epioblasma cf. *capsaeformis* (Lea, 1834), oyster mussel	X		
Epioblasma florentina walkeri (Wilson and Clark, 1914), tan riffleshell			X
Fusconaia barnesiana (Lea, 1838), Tennessee pigtoe	X	X	X
Fusconaia subrotunda (Lea, 1831), long-solid	X	X	X
Lampsilis fasciola Rafinesque, 1820, wavy-rayed lampmussel	X	X	X
Lampsilis ovata (Say, 1817), pocketbook	X		X
Lasmigona costata (Rafinesque, 1820), fluted-shell	X		
Lasmigona holstonia (Lea, 1838), Tennessee heelsplitter	X	X	
Lexingtonia dolabelloides (Lea, 1840), slabside pearlymussel	X		X
Medionidus conradicus (Lea, 1834), Cumberland moccasinshell	X		
Pleurobema oviforme (Conrad, 1834), Tennessee clubshell	X	X	X
Ptychobranchus subtentum (Say, 1825), fluted kidneyshell	X		
Villosa iris (Lea, 1829), rainbow	X	X	X
Villosa trabalis (Conrad, 1834), Cumberland bean		X	X
Villosa vanuxemensis (Lea, 1838), mountain creekshell			X

ied in abundance from rare to moderately common (Table 2). Shells of *Pleurobema oviforme* comprised 3% of all specimens collected at HR km 85.6, but was extremely rare or absent at all other localities. Only two individuals of *L. ovata* and three of *Lexingtonia dolabelloides*, both at HR km 86.5, were encountered during the July-October 1992 collecting period. *L. ovata* is moderately common throughout the upper Tennessee River system while *L. dolabelloides* is becoming increasingly rare throughout its former range in east and middle Tennessee. These two taxa, like *A. marginata* and *F. subrotunda*, had not been recorded historically from the Hiwassee River system. *E. crassidens* and *Tritogonia verrucosa* (Rafinesque, 1820) were reported from the Hiwassee River (Ortmann, 1918), but from the lower stretches in Meigs County which is now impounded by Chickamauga Reservoir. Neither species was found during this survey.

Starnes and Bogan (1988) listed *Alasmidonta viridis*, *Lasmigona holstonia* and *Villosa vanuxemensis*, all typical of headwaters, small streams and creeks, as part of the Hiwassee River mussel fauna. It should be noted, however, that the record of *V. vanuxemensis* in Starnes and Bogan (1988: 28, table 4) for the Hiwassee River is erroneous. Inadvertently the designation for this taxon was placed in the column for the Hiwassee River when it should have been assigned to the Little Tennessee River. Nevertheless, none of these three species was located in the main channel collections of the Hiwassee River in the 1992 survey. In an effort to determine the presence of mussel populations in tributaries of the Hiwassee River, several small branches and creeks were collected at one or more localities in each. It became apparent that small, spring-fed branches with rocky substrata provided unsuitable habitat for unionids. Although none of these tributaries was collected throughout its entire length, mussels were found only in Conasauga and Spring creeks. A muskrat midden in Spring Creek ca. 400 m upstream from its confluence with the Hiwassee River (HR km 69.6) contained 16 shells of *V. iris* and 186 shells of *V. vanuxemensis*. Fourteen relic specimens of the latter species were found opposite the junctions of Forest Roads (Cherokee National Forest) Nos. 27 and 2005, a straight line distance of ca. 4.0 km northeast of the creek's confluence with the Hiwassee River. Mussels were found in only one of four localities searched in Conasauga Creek (adjacent to TN Hwy. 310, ca. 4.0 km east of Etowah, McMinn County): seven relic specimens of *V. vanuxemensis*. Of the tributaries collected, Spring and Conasauga creeks appeared to provide habitat most suitable for mussels, but species diversity was low and populations localized.

Two species comprising the mussel assemblages of the Hiwassee River, HR km 105.6 to km 85.6, are included in the federal list of Endangered and Threatened Wildlife and Plants. One of these, *Villosa trabalis*, was

Table 2. Freshwater mussel species and percent of each recorded from two collection localities, Hiwassee River, Polk County, Tennessee, 1992.

Species	HR km 98.8 Specimens		HR km 85.6 Specimens	
	N	%	N	%
Alasmidonta marginata Say, 1818, elktoe	33	2.35	23	1.91
Elliptio dilatata (Rafinesque, 1820), spike	49	3.50	115	9.57
Epioblasma florentina walkeri (Wilson and Clark, 1914), tan riffleshell	-	-	16	1.33
Fusconaia barnesiana (Lea, 1838), Tennessee pigtoe	99	7.07	649	54.04
Fusconaia subrotunda (Lea, 1831), long-solid	3	0.21	11	0.91
Lampsilis fasciola Rafinesque, 1820, wavy-rayed lampmussel	38	2.71	31	2.58
Lampsilis ovata (Say, 1817), pocketbook	-	-	2	0.17
Lexingtonia dolabelloides (Lea, 1840), slabside pearlymussel	-	-	3	0.25
Pleurobema oviforme (Conrad, 1834), Tennessee clubshell	1	0.07	37	3.08
Villosa iris (Lea, 1829), rainbow	1,153	82.30	15	1.25
Villosa trabalis (Conrad, 1834), Cumberland bean	25	1.78	299	24.89
TOTAL	1,401	99.99	1,201	99.98

first reported from the Hiwassee River by Ortmann (1918), who considered the species to be extremely rare throughout its range. In a technical draft of a Recovery Plan for *V. trabalis,* Ahlstedt (1983) listed 11 rivers and several creeks from which populations are, or were, known. The species appears to have been restricted to tributary streams of the Tennessee River and upper Cumberland River. We collected specimens of *V. trabalis* at both the upper (HR km 98.8) and lower (HR km 85.6) locations, as well as below Forest Road 23 (HR km 91.7), suggesting its presence throughout the section of river between the Apalachia Dam and Powerhouse. At HR km 85.6, *V. trabalis* comprised nearly 24% (N = 299) of the shells collected, an indication of a stable and viable population.

Of special significance was the discovery of a population of *Epioblasma florentina walkeri* at HR km 85.6, the area immediately above the Apalachia Powerhouse (Fig. 2). Sixteen specimens (five females and 11 males) were recovered, mostly in muskrat midden piles. Due to nacre and shell margin deterioration, seven of the specimens may be considered relics, while the other nine appear fresh enough to have been taken by muskrats during the winter/spring of 1992 (Fig. 3). Based on collection records since 1970, Neves (1991) concluded that the only known populations of *E. f. walkeri* are in the Middle Fork Holston River, Smyth and Washington counties, Virginia. These populations were based on two collection localities. However, Ahlstedt (in Neves, 1991) found five live specimens at a third locality in Smyth County, September 1985. One freshly dead specimen of *E. f. walkeri* was also recovered in the Duck River at Interstate Highway 65 bridge (Duck River km 243.0), Maury County, Tennessee, April 1988 by Ahlstedt (Neves, 1991), but its population status there is unknown. The Hiwassee River population of *E. f. walkeri,* based on recovery of 16 specimens (< 2% of 1201 shells collected in 1992 at this location), appears small and its viability questionable.

Having discovered *Epioblasma florentina walkeri* in 1992 at HR km 85.6, three subsequent collecting trips (February 5, April 24, May 12, 1993) were taken in an effort to determine the population status of this mussel. Because of high water in February and April, only a few specimens of unionids were retrieved; however, one of those was a male *E. f. walkeri* with dried tissue adhering to the shell. From late March to early May the Powerhouse was shut down for repairs; this resulted in low water levels that permitted us to search beneath large boulders and rock ledges that had previously been inaccessible. On May 12, 1993, we collected 230 specimens, but with the exception of six recently eaten individuals, all were relic shells and no *E. f. walkeri* were found. Possibly spring high-water levels restricted muskrat predation. Shells of *Fusconaia barnesiana* (N = 137) and *Villosa trabalis* (N = 50) comprised 81% of this sample. Two relic specimens of *Lexingtonia dolabelloides* and *Lampsilis ovata* were also found, bringing the totals for those species from this collection locality to six and four, respectively.

Of special interest was the recovery of a relic shell of a mature male *Villosa vanuxemensis.* As noted earlier, the section of Hiwassee River between Apalachia Dam and Powerhouse appears to be suitable habitat for this species, but for whatever reason(s) it has failed to establish viable populations. In addition, a badly fragmented and eroded shell of *Anodonta imbecillis* was found beneath a rock ledge in one of the deeper pools. Habitat for this species is marginal and its occurrence in the Hiwassee River at this

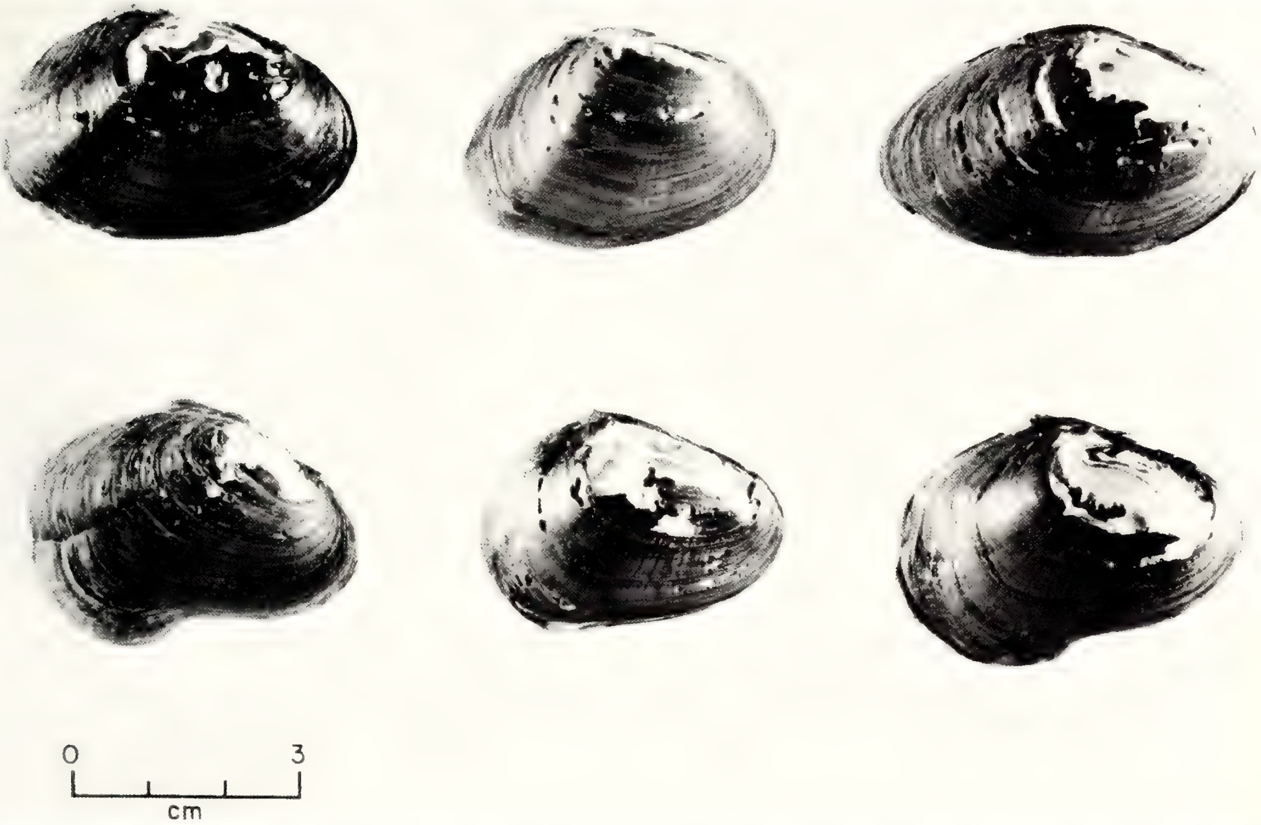

Fig. 3. Examples of male (top row) and female (bottom row) *Epioblasma florentina walkeri* from the Hiwassee River (HR km 85.6-86.0), Polk County, Tennessee.

locality is considered fortuitous.

DISCUSSION

The historic Hiwassee River might be thought of as a unit, a body of contained waterways flowing from the Blue Ridge physiographic province into the Ridge and Valley physiographic province and then into the Tennessee River. Yet several modifications have altered that continuity. First, Apalachia Dam impounds the river at HR km 105.6 forming Apalachia Lake upstream. At that point most of the water is diverted downstream to HR km 85.6, altering the river downstream from Apalachia Dam from a mediumsized river to a first-order stream.

At HR km 85.6 the diverted water from Apalachia Lake again joins the watershed as a result of water passing through the turbines at the Apalachia Powerhouse. Extremely fast currents and turbulent rapids prevail, abruptly transforming a warm-water Hiwassee River into a trout stream for 44.0 km. At ca. HR km 41.6 the river is impounded by the backwaters from Chickamauga Reservoir for the remainder of its course. Basically, there are two mussel assemblages in this river, one occurring in the unaltered stretch and the other in the lower impounded reaches.

The paucity of specimens encountered thus far by malacologists in this 44.0 km stretch of river below the Powerhouse suggests that only rarely do individuals now become established, and viable populations are apparently nonexistent. On several collecting trips to the Hiwassee River (March 16, May 10-11, 1975; August 23, 1978; August 16, 1980) between HR km 58.5 and 72.8, S. A. Ahlstedt (pers. comm., 1992) obtained only 11 specimens representing eight taxa. These species included *Fusconaia barnesiana* (N = 2); *Elliptio crassidens* (N = 1); *E. dilatata* (N = 2); *Lampsilis ovata* (N = 1); *Pleurobema oviforme* (N = 2); *Plethobasus cyphyus* (Rafinesque, 1820) (sheepsnose) (N = 1); *Potamilus alatus* (Say, 1817) (pink heelsplitter) (N = 1); *Villosa vanuxemensis* (N = 1). Except for one live *P. oviforme*, all others were badly eroded relic shells. It should be noted, however, that the lower section of the Hiwassee River, near and into the impounded portion (Chickamauga Reservoir), does support populations of several species, *e.g.* those belonging to the genera *Anodonta* Lamarck, 1799, and *Potamilus* Rafinesque, 1818.

Based on pre-impoundment and pre-powerhouse species distribution records provided by Ortmann (1918), Starnes and Bogan (1988) listed 12 freshwater mussel taxa for the entire Hiwassee River system. Their number included three forms each of *Pleurobema oviforme* and *Fusconaia barnesiana*. Ortmann (1918) also noted the presence of *Lampsilis fasciola* in the Hiwassee River, but it was omitted in the Starnes and Bogan (1988) list. In the case of *Elliptio dilatata*, Ortmann (1918: 556) commented that it was "...possibly the most widely distributed species in the upper Tennessee region, so that it is hardly required to name special localities." By including *E. dilatata*, 11 nominal species by our count comprised the mussel assemblage known to Ortmann (1918) in the Hiwassee River. Table 1 lists the eight species that Ortmann (1918) specifically collected in the Hiwassee River, Polk County, Tennessee.

Shells of 18 freshwater mussel taxa recovered during the 1986-1987 archaeological excavations at Hiwassee Old Town, a former Cherokee village (but including some prehistoric Late Woodland features) comprising an area of approximately 140 ha along the Hiwassee River (HR km 65.6-68.8), Polk County, provided noteworthy comparative data with known historic assemblages (Table 1). All of the species represented at this aboriginal site are characteristic of small- to medium-sized tributaries of the upper Tennessee River system; eight of the 17 taxa identified from the Hiwassee Old Town samples have not been reported from modern collections. Of the 94 identifiable valves recovered, those of four species, *Fusconaia barnesiana*, *F. subrotunda*, *Epioblasma* cf. *capsaeformis*, and *Ptychobranchus subtentum* comprised 65% of the samples.

Indication of prehistoric diversity is also reflected in shell samples recovered from two late prehistoric (Mississipian: A.D. 1400-1500) aboriginal sites (Table 3). During archaeological salvage operations along the Tennessee River and lower Hiwassee River from 1936-1939 prior to completion of the Chickamauga Dam (1940), field crews supplied by the federal Works Progress Administration (WPA) carried out the excavations. Although not extensive, shell samples recovered at two late prehistoric sites [Ledford Island, 40BY13 (Bradley County), HR km 20.2; Mouse Creek, 40MN3 (McMinn County), HR km 24.0] provided additional records of species inhabiting the Hiwassee River prior to impoundment. Of the 20 taxa identified from 167 valves (Table 3), 11 species are no longer a component of the known extant fauna or were not found in archaeological sites upstream.

Combining the taxa reported in the literature (Ortmann, 1918; Starnes and Bogan, 1988) with those identified from Ledford Island, Mouse Creeks and Hiwassee Old Town, and those presently inhabiting the unimpounded stretches, a minimum of 35 species are now known from the Hiwassee River.

Pre-impoundment collections of the mussel fauna in the Hiwassee River were few in number, and published species accounts appeared in regional narrations (*e.g.* Ortmann, 1918) rather than in a publication dealing only with the assemblage of the Hiwassee River. Numerous

Table 3. Freshwater mussels identified from two late prehistoric aboriginal sites along the lower Hiwassee River, Tennessee. Surface collections/ no provenience.

Species	Ledford Island (40BY13) WPA 1936-1939	Ledford Island (40BY13) PWP/MHH 1993	Mouse Creek (40MN3) WPA 1936-1939
Actinonaias ligamentina (Lamark, 1819), mucket	8	-	9
Amblema plicata (Say, 1817), threeridge	2	1	-
Cyclonaias tuberculata (Rafinesque, 1820), purple wartyback	-	-	1
Dromus dromas (Lea, 1834), dromedary pearlymussel	3	4	8
Elliptio crassidens (Lamarck, 1819), elephant-ear	3	3	1
Elliptio dilatata (Rafinesque, 1820), spike	28	11	13
Epioblasma torulosa (Rafinesque, 1820), tuberculed blossum	2	-	-
Fusconaia subrotunda (Lea, 1831), long-solid	10	13	5
Lampsilis ovata (Say, 1817), pocketbook	11	-	-
Lexingtonia dolabelloides (Lea, 1840), slabside pearlymussel	3	4	1
Ligumia recta (Lamarck, 1819), black sandshell	2	-	-
Plethobasus cooperianus (Lea, 1834), orange-foot pimpleback	-	-	1
Plethobasus cyphyus (Rafinesque, 1820), sheepnose	-	2	-
Pleurobema clava (Lamarck, 1819), clubshell	3	2	-
Pleurobema cordatum (Rafinesque, 1820), Ohio pigtoe	3	-	-
Pleurobema plenum (Lea, 1840), rough pigtoe	-	1	-
Potamilus alatus (Say, 1817), pink heelsplitter	-	1	-
Ptychobranchus fasciolaris (Rafinesque, 1820), kidneyshell	-	-	1
Ptychobranchus subtentum (Say, 1825), fluted kidneyshell	2	-	2
Quadrula sparsa (Lea, 1841), Appalachian monkeyface	1	-	-
TOTAL	81	43	43

archaeological excavations of aboriginal sites along the river were undertaken prior to dam construction in the late 1930s; however, when samples of shell were retained, they were meager. Had greater quantities of shell been saved, they would have provided a more comprehensive list of the former Hiwassee River mussel taxa than now exists. The diversity of naiad species that probably occurred in the Hiwassee River may never be known.

SUMMARY AND CONCLUSIONS

There are extremely few stretches of medium-sized and large rivers in Tennessee that contain diverse mussel assemblages reminiscent of pre-impoundment conditions. Dam construction has brought about major adverse changes in molluscan faunas with the formation of reservoirs and resulting changes in water depth and temperature, current, substratum, and amount of dissolved oxygen, as well as possible loss of fish hosts for glochidia. Pre-impoundment anthropogenic changes have also dealt a blow to mussel diversity as reflected in the differences in prehistoric mussel richness as opposed to a historic pre-impoundment decrease in species richness.

The Hiwassee River typifies these changes throughout most of its course in North Carolina and Tennessee. One short stretch, however, between the Apalachia Dam and Apalachia Powerhouse (HR km 85.6-105.6), because it is relatively unaffected by the dam, serves as a refugium for numerous mussel species known to have inhabited much of the river prior to impoundment. Of the 13 taxa represented in our 1992-1993 collections, two (*Epioblasma florentina walkeri* and *Villosa trabalis*) are included on the federal list of Endangered and Threatened Wildlife and Plants. A third species, *Lexingtonia dolabelloides,* rare in the Hiwassee River, has been proposed by the U.S. Fish and Wildlife Service as a candidate to receive protection under the Endangered Species Act of 1973 (Biggins, 1992).

Freshwater mussel species identified from shells recovered from aboriginal sites, including those reported in the literature and known presently (1993) to inhabit free-flowing sections of the Hiwassee River, total 35 taxa. Parmalee *et al.* (1982) noted the occurrence of *Anodonta imbecillis, A. suborbiculata* Say, 1831, and *Potamilus ohiensis* (Rafinesque, 1820) at the impounded mouth of the Hiwassee River at its confluence with the Tennessee River (Chickamauga Reservoir). Although one or a few additional species may eventually become established or discovered in the lower impounded section of the Hiwassee River, little if any change is anticipated in mussel assemblages extant in Apalachia Lake upstream from Apalachia Dam and in the cold fast-flowing stretch of river downstream from the Apalachia Powerhouse. The section of Hiwassee River between the Apalachia Dam and Powerhouse is unique, providing stable and basically pristine mussel habitat. It should receive both state and federal protection to preserve extant plant and animal communities, and be considered as a possible location for transplanting other threatened or endangered mollusks when techniques for such transplants are perfected.

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Life history of the endangered James spinymussel *Pleurobema collina* (Conrad, 1837) (Mollusca: Unionidae)

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Abstract. The reproductive period, host fish requirements, and population characteristics of the James spinymussel [*Pleurobema collina* (Conrad, 1837)] were studied from 1987 to 1989 in the James River drainage, West Virginia and Virginia. This summer brooder was gravid from late May through early August and released the majority of glochidia in early June through late July. The mean fecundity was roughly 13,000 brooded eggs/female. Observations in the field and laboratory implicated fishes of the Cyprinidae as hosts for glochidia of the James spinymussel. Induced infestations of glochidia on fishes in the laboratory confirmed seven host species: the bluehead chub [*Nocomis leptocephalus* (Girard)], rosyside dace (*Clinostomus funduloides* Girard), satinfin shiner [*Cyprinella analostana* (Girard)], rosefin shiner [*Lythrurus ardens* (Cope)], central stoneroller [*Campostoma anomalum* (Rafinesque)], blacknose dace [*Rhinichthys atratulus* (Hermann)], and mountain redbelly dace [Phoxinus oreas (Cope)]. The age class structure of two populations, obtained by thin-sectioning valves collected in muskrat middens, ranged from 3 to 19 yrs with evidence of strong and weak year classes. Incidence of spines differed significantly among populations. The mean annual mortality rate of adults was 15.6 ± 1.4%.

The James spinymussel [*Pleurobema collina* (Conrad, 1837)] is one of three spined species of freshwater mussels in the United States (Fig. 1). The historic range of this species, endemic to the James River watershed, is thought to have occurred upstream of Richmond, Virginia, throughout the larger tributaries of the river basin. However, a survey on the status of this species in 1984 revealed its occurrence in only two small tributaries to the James River, an approximately 90% reduction in range (Clarke and Neves, 1984). As a result of this reduction in range and its rarity, the James spinymussel was listed by the federal government as endangered in July 1988. Additional populations have been reported since its federal listing (Hove, 1990).

As with most endemic mussel species, little is known of the life history and ecology of the James spinymussel. Boss and Clench (1967) described various anatomical characteristics and sexual dimorphism of *Pleurobema collina*. They suggested that it was probably a short-term brooder, releasing glochidia in the summer. Habitat of *P. collina* included streams ranging in size from 3 to 23 m wide and 15 to 100 cm deep (Clarke and Neves, 1984). The species occupied sediments of cobble and sand in reaches with slow to moderate currents. The spinymussel occurred historically in larger streams such as the James River opposite the city of Maidens where the river is about 150 m wide (museum records, Ohio State University). Other aspects of its biology were unknown. The purpose of this study, therefore, was to determine the reproductive period, required fish hosts, and population characteristics of the James spinymussel in the headwaters of the James River, West Virginia and Virginia.

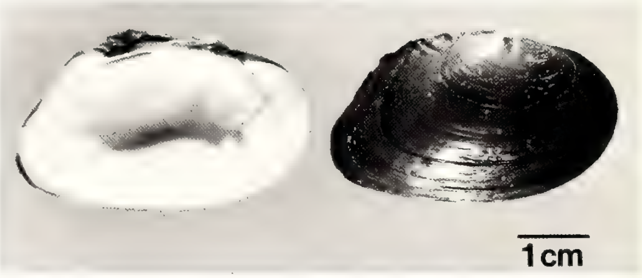

Fig. 1. *Pleurobema collina* from Craig Creek, Virginia.

MATERIALS AND METHODS

Three populations of *Pleurobema collina* were monitored weekly during spring 1988 and 1989 to determine the period of gravidity. These populations were in

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South Fork Potts Creek, Monroe County, West Virginia; Craig Creek, Craig County, Virginia; and Johns Creek, Craig County, Virginia. Gravidity was checked by separating the valves approximately 1 cm to observe whether the outer gills were swollen with conglutinates. Observations were made on gill coloration, degree of gill inflation, and conglutinates released by gravid females. In spring 1988, eight gravid females at the Craig Creek study site were marked by scoring the right valve. Seven of these females were collected again in spring 1989 and placed in a 0.5 x 0.5-m area to facilitate their relocation. These mussels were monitored weekly from 26 May through 8 August 1989, and the numbers of gravid and nongravid females were recorded weekly. During each sampling, five to seven of the marked females were relocated and checked for gravidity.

To determine the period of glochidial release, stream drift was sampled in 1988 at the study site in South Fork Potts Creek. Drifting glochidia were collected with square-framed drift nets (0.45 m^2) constructed of 130-micron nylon mesh fitted with removable cod-ends. Three drift nets were placed equidistantly, perpendicular to the current downstream of a 20 m long pool that held approximately 30 adult *Pleurobema collina*. Drift samples were collected for 2 hrs between 1300 and 1700 hrs from 26 May through 12 August 1988 and preserved in 10% formalin, buffered with sodium borate to prevent dissolution of glochidial valves. Drift material was examined in a gridded petri dish under a dissecting microscope (25-40x), and glochidia were counted. Because the mussel fauna of South Fork Potts Creek consisted only of the squawfoot [*Strophitus undulatus* (Say, 1817)] and *P. collina*, glochidia of *P. collina* were readily identified by their smaller size and lack of hooks. Cross-sectional area of the stream, and the velocity of surface water 5 m downstream of the sampling site were used to estimate discharge. Densities of glochidia were computed from measurements of water depth and velocity at the net opening and from counts of glochidia/sample. A 90-day Ryan thermograph (Model J) recorded temperature continuously from 30 May to 14 July 1988.

The determination of probable fish hosts was initiated by examination of fishes collected by electrofishing in South Fork Potts Creek in spring and summer 1988. Weekly collections of fishes began on 23 May 1988 when gravid *Pleurobema collina* were first observed. Fishes were collected from a 50-m reach of stream below the drift sampling site. The collection and examination of fishes continued through 4 August 1988. Captured fishes were anesthetized, identified, visually inspected on the gills for glochidial infestations, and returned to the stream. Incidence of glochidial attachment was recorded.

Laboratory experiments were conducted to confirm the identification of fish hosts of *Pleurobema collina*. Fishes were collected from streams outside of the James River drainage to eliminate the possibility of acquired immunity from prior exposure to glochidia (Neves *et al.*, 1985). Test species were collected with backpack electroshocker and by seining. Collected fishes were held at 16-23^{o} C in test aquaria (40 l and 96 l capacity), at least 5 d prior to infestation.

Mature glochidia were obtained from collected gravid females that were subsequently returned to their natal stream. When gravid females were brought into the laboratory, they were held at room temperature (approximately 25^{o} C) or in a recirculating circular stream (approximately 15^{o} C). Mussels transported to the laboratory were held in beakers to ensure containment of glochidia. Females either released their conglutinates naturally within three to nine days or aborted them after handling. Glochidia were separated from aborted conglutinates by gently drawing the conglutinates in and out of a pipette. The procedures for infestation, subsequent examination of fishes, and recovery of juveniles were performed according to Zale and Neves (1982) with one exception. American eels [*Anguilla rostrata* (Lesueur)], because of difficulty in handling, were infested by placing them in 100 ml of water with 300 to 600 glochidia under vigorous aeration for seven to nine min. The effectiveness of this technique was confirmed on four swallowtail shiners [*Notropis procne* (Cope)] prior to testing the eels. Juvenile mussels were identified by their opaque, dimpled valves and by their foot movements. A fish was considered a host if encystment and metamorphosis to the juvenile stage occurred.

POPULATION CHARACTERISTICS

Twenty-three *Pleurobema collina* were marked on 20 June 1988 upstream of the study site on South Fork Potts Creek to verify that growth lines formed annually. The specimens were given a unique mark, and the edges of their valves were double-notched to identify the 1988 annulus. The number of annuli, total length, and mark for each mussel were recorded. In late summer and fall 1989, these mussels were retrieved and inspected for recent annual growth rings.

The ages of the specimens were determined by thin sectioning of valves with the technique described by Neves and Moyer (1988). Valves of *Pleurobema collina* were collected from muskrat middens at Johns Creek and its tributary Dicks Creek in Craig County, Virginia. One hundred paired valves were sectioned, then aged using a dissecting microscope. Each valve was aged at least three times to provide a precise estimate. A von Bertalanffy growth equation was computed from length-at-age data and was fit by nonlinear procedures to derive the parameters of the equation (SAS Institute, 1982). The annual mortality rate (M) for 97 of the adult mussels (ages 4-19) collected in muskrat middens was computed using the estimator of Robson and Chapman (1961):

$$M=1-T/(\sum N_x+T-1))$$

$$\text{Variance} = (T/\sum N_x+T-1)) \times ((T/\sum N_x+T-1))-((T-1)/\sum N_x+T-2)))$$

where N_x is the number in each successive age class (x) and $T = N_1 + 2N_2 + 3N_3 + \ldots XN_x$. This estimator assumes constant cohort recruitment and survival rate, and equal vulnerability of adults to muskrat predation.

Because the incidence of spines was seemingly variable among streams sampled in the upper James River watershed, we tested these differences using multiple comparisons for population proportions (Zar, 1984). Presence of spines on valves collected from Dicks, Johns, South Fork Potts, Craig, and Catawba creeks was compared.

Common and scientific names for mussels and fishes are according to Turgeon *et al.* (1988) and Robbins *et al.* (1991).

RESULTS

REPRODUCTIVE PERIOD

The period of gravidity of *Pleurobema collina* was nearly the same in 1988 and 1989 (Table 1). Gravid females of *P. collina* in South Fork Potts Creek were collected between 23 May and 9 August 1988, and between 23 May and 8 August 1989. Limited surveys in Johns and Craig Creeks in 1988 located gravid *P. collina* on 30 May in Craig Creek and between 27 June and 4 July in Johns Creek. In 1989, gravid females were observed in Craig Creek between 26 May and 11 July. The period of gravidity of the James spinymussel was longer in South Fork Potts Creek in 1989 than in either Johns Creek or Craig Creek.

Efforts to determine the peak of the gravidity period were hampered by two weeks of high flows in early June 1989. On 26 May 1989, five of the eight females marked in 1988 were examined at the Craig Creek study site, and one of them was gravid. On 3 June, two more marked females were found and placed with the others. On this day, five of the seven females were gravid. During the following two weeks (9-23 June), the water was so murky or the current so swift that the marked females could not be collected for examination. The females were checked again on 27 June, and only two of the six examined were gravid. The marked females were examined again on 4 and 11 July, but none was gravid. Gravidity apparently peaked in mid-June during the high flow period.

Table 1. Gravidity of female *Pleurobema collina* at study sites in Craig, Johns and South Fork Potts Creeks in 1988 and 1989.

Collection date	Study site	Number examined	Number gravid	Percentage of females gravid[1]
1988				
12 May	Johns Creek	1	0	
23 May	S. Fk. Potts Creek	36	15	
30 May	Craig Creek	18	10	
27 June	Johns Creek	8	6	
04 July	Johns Creek	6	4	
11 July	S. Fk. Potts Creek	15	4	
14 July	S. Fk. Potts Creek	5	2	
25 July	S. Fk. Potts Creek	16	7	
09 August	S. Fk. Potts Creek	11	11	
12 August	S. Fk. Potts Creek	8	0	
1989				
23 May	S. Fk. Potts Creek	8	5	
26 May	Craig Creek	6	1	20%
		10	2	
03 June	Craig Creek	6	5	83%
	S. Fk. Potts Creek	12	1	
06 June	S. Fk. Potts Creek	7	2	
27 June	Craig Creek	6	2	33%
04 July	Craig Creek	7	1	14%
11 July	Craig Creek	7	0	0%
16 July	S. Fk. Potts Creek	8	5	
28 July	S. Fk. Potts Creek	17	5	
08 August	S. Fk. Potts Creek	2	1	

[1] Females marked in 1988.

RELEASE OF GLOCHIDIA

Drift sampling in 1988 provided a record of the changes in glochidial density with stream discharge (Table 2). Only individual glochidia (no conglutinates) were collected in drift nets. Glochidial densities peaked twice, once in late June (9.6 glochidia/m^3) and again during mid-July (15.9 glochidia/m^3). The mean summer water temperature stabilized around 23° C (Fig. 2). The densities of glochidia increased three days after the flow approached the mean summer level of 0.05 m^3/sec on 23 June.

Valves of the glochidia of *Pleurobema collina* are subovate and symmetrical. The exterior surface is smooth with very few pits. Glochidia are transparent and colorless, and the dorsal hinge is slightly convex. No significant difference was evident in length, height, and hinge length of glochidia from South Fork Potts and Craig Creeks (p-values: length = 0.39, height = 0.28, hinge length = 0.29). The length of valves ranged from 0.18 to 0.22 mm (mean ± 1 SD = 0.19 ± 0.01 mm), and the height of valves ranged from 0.14 to 0.20 mm (0.17 ± 0.01 mm). The hinge length of the valves ranged from 0.10 to 0.16 mm (0.13 ± 0.01 mm). The adductor muscle is attached to approximately 15% of the inside surface area of the valve and is just dorsal and anterior to the valve's center.

Early in the gravidity period, the outer gills of females became significantly enlarged. As the glochidia matured, conglutinates changed color, and the hue of the gills changed from creamy white to pale gray or tan. Released conglutinates were subcylindrical, thin, and compressed. A tan-colored row of pigmentation occurred down the center of the conglutinate, and the glochidia were arranged in two staggered rows around its perimeter. The tips of the conglutinates were usually rounded. One to three conglutinates from each of 25 females from South Fork Potts and Craig Creeks ranged from four to 14 mm long (8.7 ± 3.0 mm) and from one to 1.5 mm (1.0 ± 0.1 mm) wide. Some of the conglutinates were V-shaped, consisting of two conglutinates joined at one end. Pigmentation varied among conglutinates and within females, from nonpigmented to fully pigmented. Prematurely released conglutinates from two females were unusually pale and curled into circular or helical shapes.

Table 2. Water temperature, stream discharge, and density of *Pleurobema collina* glochidia in South Fork Potts Creek, 1988.

Sample date	Daily median temperature ($^{\circ}$C)	Discharge (m^3/sec)	Glochidial density (N/m^3)
26 May	18	–	0
30 May	14	–	0
03 June	19	0.446	<1
06 June	16	0.209	<1
10 June	21	0.148	0
13 June	15	0.106	0
20 June	21	0.031	0
23 June	23	0.050	6.7
27 June	24	0.013	9.6
30 June	*	0.025	5.6
05 July	*	0.010	0
08 July	25	0.010	1.6
11 July	25	0.012	15.9
14 July	24	0.024	0
18 July	*	0.020	0
21 July	*	0.038	0
25 July	*	0.025	<1
02 August	*	0.035	0
04 August	*	0.033	0
09 August	*	0.015	0
12 August	*	0.022	0

*Thermograph failure.

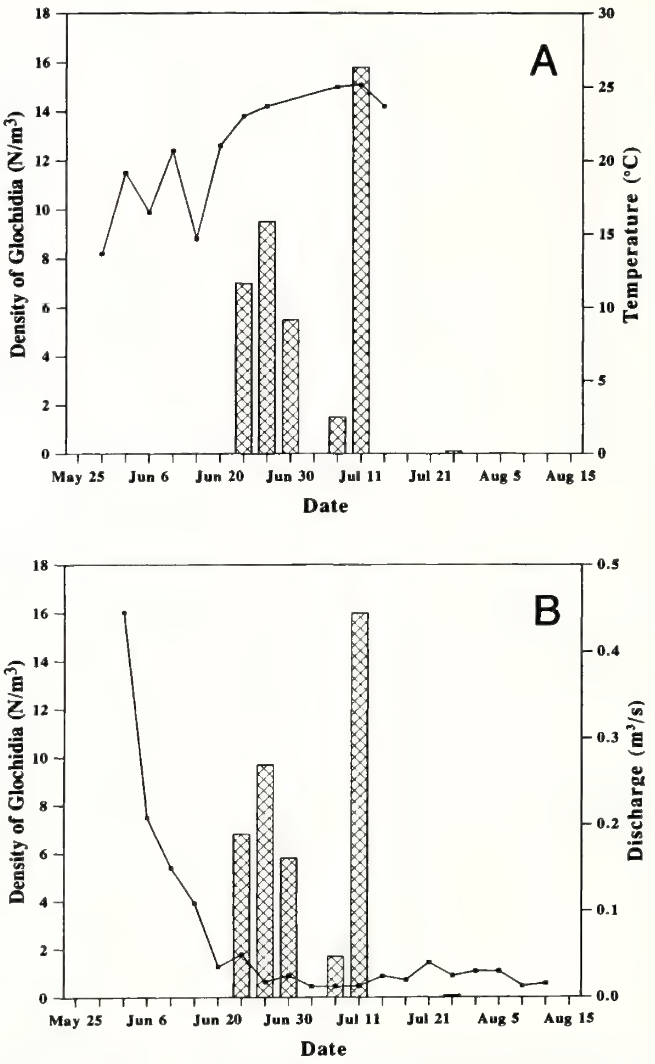

Fig. 2. Densities of *Pleurobema collina* glochidia in stream drift, with accompanying water temperature (A) and discharge data (B).

An estimate of mean fecundity was obtained from a sample of 28 gravid females that released conglutinates in

Table 3. Numbers of released conglutinates, glochidia, and unfertilized eggs per conglutinate from female *Pleurobema collina* collected in South Fork Potts and Craig Creeks.

Date released	Collection site	Number of conglutinates	Number of glochidia	Number of unfertilized eggs
1988				
08 June	S. Fk. Potts Creek		45 66	4 3
09 June	S. Fk. Potts Creek	137	69 96	7 12
09 June	Craig Creek	122	92 112	6 12
23 June	S. Fk. Potts Creek	109	78 85	6 5
23 June	S. Fk. Potts Creek	110		
02 July	Johns Creek	106		
05 July	Johns Creek	90		
13 July	S. Fk. Potts Creek	113	100 100	7 11
1989				
05 June	Craig Creek	124	128 134	6 6
05 June	Craig Creek		135 114	10 7
13 June	S. Fk. Potts Creek	168		
16 June	S. Fk. Potts Creek	150		
11 July	S. Fk. Potts Creek		158 102	14 11
	Means	123	101	8

captivity. During 1988 and 1989, ten females released between 90 and 168 conglutinates (123 ± 23.1) in the laboratory (Table 3). Preserved samples of conglutinates from eight of the 28 females were suitable for counting glochidia. The number of glochidia in two conglutinates from each of these females ranged from 45 to 158 (101 ± 29.2). Mean fecundity/female, to include glochidia (12,423) and unfertilized eggs (984), therefore was 13,407 ± 3,986.

FISH HOST DETERMINATIONS

Fourteen of the 21 fish species known to inhabit South Fork Potts Creek were examined for glochidial infestations during the drift sampling period in 1988 (Table 4). Glochidia were observed on common shiners, rosyside daces, bluehead chubs, pumpkinseeds, and fantail darters. No glochidia were observed on central stonerollers, redbreast sunfishes, longfin darters, rock basses, margined madtoms, smallmouth basses, creek chubs, northern hog suckers, or white suckers. The frequency of glochidial infestation was high on common shiners, rosyside daces, and bluehead chubs (Table 4).

Successful attachment of *Pleurobema collina* glochidia to fishes in laboratory infestations was low. Although 35 to 65 glochidia were placed directly on the gills, only three to 18 glochidia remained attached one hr later. However, once attached to a host, most glochidia

Table 4. Incidence of *Pleurobema collina* glochidial infestations on fishes collected in South Fork Potts Creek, 26 May through 4 August 1988.

Fish species	Number inspected	Percent infested
Cyprinidae		
Luxilus cornutus (Mitchell) (common shiner)	50	32
Clinostomus funduloides Girard (rosyside dace)	5	20
Nocomis leptocephalus (Girard) (bluehead chub)	183	19
Campostoma anomalum (Rafinesque) (central stoneroller)	81	0
Semotilus atromaculatus (Mitchill) (creek chub)	3	0
Centrarchidae		
Lepomis gibbosus (Linné) (pumpkinseed)	8	12
Lepomis auritus (Linné) (redbreast sunfish)	45	0
Ambloplites rupestris (Rafinesque) (rock bass)	9	0
Micropterus dolomieu Lacepède (smallmouth bass)	6	0
Percidae		
Etheostoma flabellare Rafinesque (fantail darter)	40	8
Etheostoma longimanum Jordan (longfin darter)	13	0
Ictaluridae		
Noturus insignis (Richardson) (margined madtom)	6	0
Catostomidae		
Hypentelium nigricans (Lesueur) (northern hog sucker)	2	0
Catostomus commersoni (Lacepède) (white sucker)	1	0
Total	452	

remained on the fish throughout the metamorphosis period. A fish species was considered a host of *P. collina* if attachment, encystment, and metamorphosis to the juvenile stage resulted. Several fish species experienced high mortality and subsequently were retested. Seven species of cyprinids were identified as suitable hosts of *P. collina* and included the bluehead chub, rosyside dace, satinfin shiner, rosefin shiner, central stoneroller, blacknose dace, and mountain redbelly dace (Table 5). The bluehead chub produced the greatest mean number of juveniles/individual (10.2), and the mountain redbelly dace produced the fewest (0.62). Variation in the number of juveniles produced during each trial was due primarily to differences in the initial number of attached glochidia. Ten of the 11 tested fish families were unsuitable as hosts of *P. collina* glochidia (Table 6). Other cyprinid species in the upper James River drainage, although untested, also may be suitable hosts.

Relatively few glochidia were collected from the aquaria with white suckers and northern hog suckers the day after inoculation. The suckers quickly sloughed the glochidia and apparently consumed them. These observations lead us to believe that suckers and other benthic feeders may ingest glochidia incidentally in streams.

Several nonhost fish species retained glochidia for a longer period of time than other nonhost fish, but only empty valves identical to those of living juveniles were collected. Kitchel (1985) described this phenomenon and called the embryonic mussels pre-metamorphosed juveniles. In our study, pre-metamorphosed juveniles were occasionally produced by host species, and by fish species which did not produce viable juveniles. Because of delayed metamorphosis of glochidia at colder water temperatures, the pre-metamorphosed juveniles observed in our study may have been due in part to the relatively cold water temperatures (13-15° C) of the 1989 host fish experiments. Due to the lengthy periods of attachment to these species, a repeat of these infestations seems warranted to confirm their nonhost designations.

POPULATION CHARACTERISTICS

On 28 July and 2 December 1989, ten of 23 *Pleurobema collina* marked on 20 June 1988 were recovered and examined for annulus formation. The recovered specimens were between six and ten years old, and two to eight mm of growth were added to the margin of each valve. One of the six mussels had a second thin growth check between the 1988 annulus and the margin; however, all others exhibited only one annulus.

Age class structure of 100 specimens of *Pleurobema collina* collected from muskrat middens along Johns and Dicks Creeks ranged from three to 19 years, with a mean age of eight years (Fig. 3). The age distribution is slightly bimodal but indicated that sufficient recruitment is sustaining these populations. The presence of dominant year-classes, such as age 11, was evident. The estimated mean annual mortality rate was 15.6 ± 1.4% for adult mussels (ages 4-19).

The growth pattern in valve length of *Pleurobema collina* from Johns and Dicks Creeks was asymptotic. The predicted annual growth increments declined gradually

Table 5. Cyprinid fish species that served as hosts for *Pleurobema collina* glochidia in laboratory experiments.

Fish species	Number of fish infested	Number of survivors	Juvenile[1] mussels collected	Days to metamorphosis	Temperature range ($^{\circ}$C)
Nocomis leptocephalus (Girard)	11	0	—	0	16-21
(bluehead chub)	7	4	41	48	15-18
Clinostomus funduloides Girard	13	11	—	13	15-18
(rosyside dace)	9	0	—	7	15-18
	3	14	14	30	15-18
Cyprinella analostana (Girard)	15	10	44	34	15-18
(satinfin shiner)					
Lythrurus ardens (Cope)	5	0	—	0	15-18
(rosefin shiner)	17	5	2	40	15-18
	5	5	8	36	15-18
Campostoma anomalum (Rafinesque)	16	1	13	26	16-23
(central stoneroller)					
Rhinichthys atratulus (Hermann)	15	12	3	23	16-23
(blacknose dace)	14	9	6	50	15-18
Phoxinus oreas (Cope)	9	1	1	29	16-23
(mountain redbelly dace)	17	13	8	44	15-18

[1] Includes pre-metamorphosed juveniles.

Table 6. Fish species that did not serve as hosts for *Pleurobema collina* glochidia in laboratory experiments.

Fish species	Number of fish infested	Number of survivors	Period of attachment (days)	Number of premetamorphosed juveniles	Temperature range (°C)
1988					
Catostomidae					
Catostomus commersoni (Lacepède) (white sucker)	15	15	1	—	16
Hypentelium nigricans (Lesueur) (northern hog sucker)	11	11	2	—	20
Ictaluridae					
Noturus insignis (Richardson) (margined madtom)	18	18	8	—	22-23
Percidae					
Etheostoma flabellare Rafinesque (fantail darter)	8	6	10	—	15-18
Centrarchidae					
Lepomis auritus (Linné) (redbreast sunfish)	13	11	12	—	15-18
Cyprinidae					
Notropis procne (Cope) (swallowtail shiner)	10	6	31	—	13
1989					
Percidae					
Etheostoma olmstedi Storer (tessellated darter)	1	1	6	—	13-15
Percina notogramma (Raney and Hubbs) (stripeback darter)	8	8	8	—	13-15
Centrarchidae					
Ambloplites rupestris (Rafinesque) (rock bass)	6	6	6	—	13-15
Cyprinidae					
Notropis procne (Cope) (swallowtail shiner)	4	4	55	—[1]	13
Catostomidae					
Erimyzon oblongus (Mitchill) (creek chubsucker)	8	8	2	—	13-15
Cyprinidae					
Pimephales notatus (Rafinesque) (bluntnose minnow)	9	9	12	—	13-15
Notemigonus crysoleucas (Mitchill) (golden shiner)	6	5	41	4	13-15
Umbridae					
Umbra pygmaea (DeKay) (eastern mudminnow)	6	6	12	—	13-15
Aphredoderidae					
Aphredoderus sayanus (Gilliams) (pirate perch)	7	7	37	—	13-15
Anguillidae					
Anguilla rostrata (Lesueur) (American eel)	9	8	44	1	13-15
Poeciliidae					
Gambusia affinis (Baird and Girard) (western mosquitofish)	9	9	45	119	13-15
Esocidae					
Esox niger Lesueur (chain pickerel)	9	8	25	22	13-15
Salmonidae					
Salvelinus fontinalis (Mitchill) (brook trout)	6	6	15	—	13-15

[1] Not enumerated.

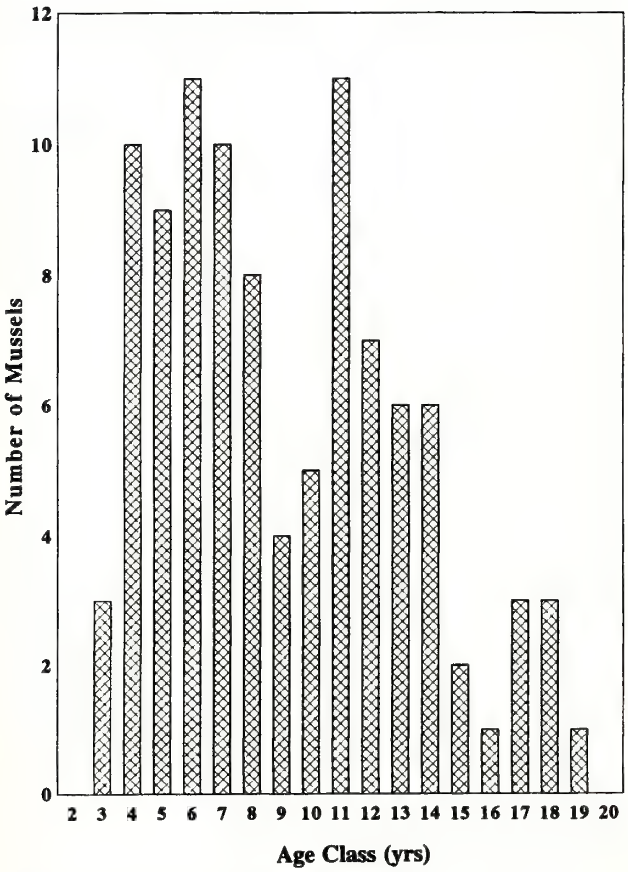

Fig. 3. Age structure of *Pleurobema collina* in Johns and Dicks creeks, based on shells collected in muskrat middens.

from 7.04 mm/yr for age 1 individuals to 0.88 mm/yr for age 19 mussels (Table 7). The von Bertalanffy growth equation that described growth of *P. collina* is as follows:

$$L_t = (74.439)(1-e^{(-0.11556(t+1.2436))})$$
$$(N = 100, MSE = 4.48)$$

The growth equation predicted a maximum length of 74.4 mm, and the largest valve collected was 75.2 mm. Observed mean length-at-annulus measurements fit most predicted values extremely well, especially the younger cohorts (Table 7). The small sample sizes of older age groups likely resulted in the poorer fit between observed and predicted values for these cohorts.

The occurrence and location of spines on *Pleurobema collina* varied considerably among populations and individuals within populations (Fig. 4). The incidence of spines differed significantly among the five populations ($p = 0.05$). Incidence of spines was significantly lower in Dicks Creek and higher in Catawba Creek than in the other three streams, which were not significantly different ($p = 0.05$). Most valves and live mussels from these populations lacked spines, or evidence of spines at younger ages such as nubs or erosive scars where spines should have been visible. The presence of spines in juvenile and adult mussels in most headwater populations was the exception rather than the rule.

DISCUSSION

The habitat requirements of the James spinymussel are seemingly nonspecific. The mussel was found in 1.5 to 20 m wide second and third order streams at water depths of 0.3 to 2 m. *Pleurobema collina* was found in a variety of substrata ranging from sand and silt mixtures to gravel and sand mixed with embedded rubble. Specimens occurred in a variety of flow regimes, near stagnancy in some pools to swift water in riffles and runs. These occupied habitats are similar to those described by Clarke and Neves (1984).

The microhabitat requirements of the other species of spinymussels seem to be more restrictive than those of the James spinymussel. The Altamaha spinymussel [*Elliptio spinosa* (Lea, 1836)] has been found only on sandbars of very coarse to fine sand (Sickel, 1981). The Tar spinymussel (*E. steinstansana* R. I. Johnson and Clarke, 1983) also lives in hard-packed, fine to coarse sand substrata and is occasionally found in soft sand (Clarke, 1983; Widlak 1987). Although the James spinymussel was often found in sandy habitats, it also resided in gravel and embedded rubble. The James spinymussel is somewhat nonspecific in its habitat requirements and now occurs primarily in headwater streams. Habitats occupied by the Altamaha and Tar spinymussels might also include coarser substrata in the headwaters of their respective drainages, but these two species are seemingly adapted only to finer

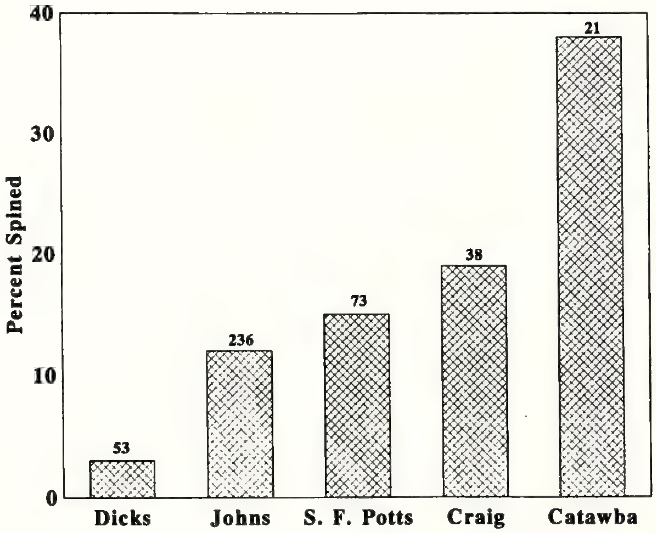

Fig. 4. Incidence of spines on *Pleurobema collina* from five populations in the upper James River watershed. Number on histogram is sample size for each population.

Table 7. Observed and predicted lengths-at-annuli (mm) of *Pleurobema collina* from Johns and Dicks Creeks, Craig County, Virginia, 1988 and 1989.

Annulus	Number of individuals	Observed length		Predicted length	Growth increment
		Mean	Range		
0	0	—	—	9.96	
1	0	—	—	17.00	7.04
2	0	—	—	23.27	6.27
3	3	28.68	25.00-34.40	28.85	5.58
4	10	33.83	27.35-39.25	33.83	4.98
5	9	39.30	35.25-42.70	38.26	4.43
6	11	42.60	37.45-48.90	42.21	3.95
7	10	43.80	40.35-48.75	45.73	3.52
8	8	49.36	44.40-56.20	48.86	3.13
9	4	49.29	43.60-53.30	51.65	2.79
10	5	54.41	47.55-58.20	54.14	2.49
11	11	57.81	50.55-65.55	56.35	2.21
12	7	60.31	53.10-75.20	58.33	1.98
13	6	61.47	7.80-64.25	60.08	1.75
14	6	61.98	58.25-65.70	61.65	1.57
15	2	64.20	61.25-67.15	63.05	1.40
16	1	60.85	60.85	64.29	1.24
17	3	61.83	58.15-64.30	65.40	1.11
18	3	65.27	62.15-68.80	66.38	0.98
19	1	71.35	71.35	67.26	0.88

substrata. The spines of the Altamaha and Tar spinymussels are generally more developed than those of the James spinymussel, and if they act as stabilizers in shifting substrata such as loose sand (Johnson, 1970), the spines may be morphological evidence of their habitat specificity.

GLOCHIDIAL RELEASE AND GRAVIDITY PERIODS

Like the other members of its genus, *Pleurobema collina* is a short-term brooder that releases glochidia from early June through late July. Weaver (1981) reported glochidia of *P. oviforme* (Conrad, 1834) and *Fusconaia barnesiana* (Lea, 1838) in drift samples from mid-May through late July 1980 in Big Moccasin Creek, Virginia, and Kitchel (1985) recorded gravid *P. oviforme* from mid-June through late August in the North Fork Holston River, Virginia. Yokley (1972) reported the glochidial release period of *P. cordatum* (Rafinesque, 1820) from late April through early July, with peak glochidial densities in June in the upper Tennessee River.

Water temperature and stream discharge are thought to be important environmental variables that influence the glochidial release and gravidity periods. The peak of the glochidial release period of *Pleurobema* spp. occurs when mean daily water temperatures are between 21° and 29° C in late spring and early summer (Yokley, 1972; Kitchel, 1985). Peak densities of *P. collina* glochidia were found in South Fork Potts Creek after stream temperatures reached 23° C. This finding is similar to that reported for other congeneric mussels. Glochidial density of *P. cordatum* peaked in the Tennessee River in June after the water temperature averaged 21° C (Yokley, 1972). *Pleurobema oviforme* glochidia reached peak densities at 24° C in Big Moccasin Creek, Virginia (Weaver, 1981). In the North Fork Holston River, *P. oviforme* glochidia reached peak densities in mid- and late July when temperatures were between 25° and 29° C (Kitchel, 1985).

Stream discharge could have influenced the glochidial release period because glochidial densities peaked three days after the spring discharge dropped to near-normal summer levels in South Fork Potts Creek. A seasonal rise in discharge and a subsequent increase in nutrient levels were described by Hynes (1970) to initiate reproductive activity in many aquatic animals. Kitchel (1985) suggested that discharge could influence the abundance of glochidia of various unionids in stream drift in the North Fork Holston River, Virginia. However, we collected insufficient data to correlate stream discharge with densities of glochidia.

The glochidia of all members of the genus *Pleurobema* are spineless, subovate, and of medium size (Utterback, 1915-1916; Baker, 1928; Oesch, 1984). Glochidia of *P. collina* were similar in size and shape to other members of the genus, ranging from 0.18 to 0.22 mm in length and from 0.14 to 0.20 mm in height. Glochidia of *P. oviforme* range from 0.15 mm to 0.17 mm in length and height (Weaver, 1981; Kitchel, 1985). The length and height of glochidia of *P. cordatum* are 0.15 to 0.18 mm (Utterback, 1915-1916), and the glochidia of *P. coccineum* (Conrad, 1834) are 0.15 to 0.16 mm in length and height (Utterback, 1915-1916; Baker, 1928; Clarke, 1981).

Conglutinates released by gravid females of *Pleurobema collina* were unlike those described for congeneric species. Mature conglutinates were subcylindrical and compressed, and glochidia were arranged along the perimeter of each conglutinate. Pigmentation consisted of a thin ribbon of tan color in the center of the conglutinate, although some conglutinates were colorless. The conglutinates of other *Pleurobema* spp. are thin, lanceolate, or leaf-shaped, varying in color from white to yellow or orange (Oesch, 1984), and glochidia typically are spread throughout the conglutinate. Because the James spinymussel is the only species of *Pleurobema* on the Atlantic slope, placement of the species in this genus could need to be re-evaluated. The evolutionary significance of conglutinates is unknown, although some researchers suggested that they could mimic food items of fishes when released (Chamberlain, 1934; Kat, 1984; Gordon and Layzer, 1989).

The average fecundity of *Pleurobema collina* is lower than that of females of most other freshwater mussels. Freshwater mussels usually produce between 75,000 and 3,000,000 glochidia/female (Coker *et al.*, 1921). Females of *Quadrula cylindrica strigillata* (Wright, 1898) produce about 114,246 (± 5368) embryos/female (Yeager and Neves, 1986), and *Margaritifera margaritifera* (Linné, 1758) has an average fecundity of 4.2 million glochidia/female (Bauer, 1987). A female *Unio crassus* Retzius, 1788, produces between 9,500 and 100,000 glochidia, depending on its size (Engel and Hannover, 1989). Gravid *P. collina*, however, brood roughly 13,400 glochidia/female.

FISH HOSTS

Species of the genus *Pleurobema* parasitize a relatively small percentage of the fish assemblage in their respective streams. Of 14 species of fishes collected from South Fork Potts Creek, only common shiners, rosyside daces, bluehead chubs, pumpkinseeds, and fantail darters had *P. collina* glochidia attached to their gills. Although no glochidia were observed on central stonerollers, this species was identified as a fish host in laboratory experiments. A possible reason for this discrepancy is the inaccessibility of their gills. The central stoneroller has an extended connection between its gill and isthmus, and only the outermost gill and distal edges are visible when viewed through the opercular opening. Because of limited access to the gills, our observations may have overlooked infestation of this species. Among the 21 species inhabiting the South Fork Potts Creek, the incidence of infestation was 19.6% (N = 286). Similar results were obtained by an investigation of *P. oviforme* in the North Fork Holston River, Virginia. Twelve of 41 species of fishes were parasitized by glochidia of *P. oviforme* (see Kitchel, 1985). Of the fish species infested with glochidia, 12.3% (N = 1738) bore *P. oviforme* glochidia. Most of the fish species that serve as hosts of *P. collina* are common throughout the drainage, such that the extirpation of this mussel from limited host abundance or distribution is unlikely. Cyprinids seem to be a suitable family of host fishes because they are one of the most diverse and successful lineages in North America and were probably more abundant before the introduction of non-native piscivores in the James River drainage.

POPULATION CHARACTERISTICS

The age class structure of most mussel species seemingly indicates that younger mussels are often underrepresented in population samples (Yokley, 1972; Coon *et al.*, 1977), perhaps because of sampling bias (Chamberlain, 1931; Coon *et al.*, 1977). Zale (1980) found that quadrat sampling was effective for collecting young mussels, although other researchers found this technique inadequate for rare species (Neves *et al.*, 1980; Kovalak *et al.*, 1986; Neves and Odom, 1989). Quadrat sampling would probably be suitable for obtaining young *Pleurobema collina* because we documented their occurrence in most extensively surveyed streams. We used valves from muskrat middens to assess age class composition, which may have resulted in some bias against the youngest age groups (Neves and Odom, 1989; Hanson *et al.*, 1989). However, in spite of any sampling bias in valve sizes, we documented healthy recruitment in the populations sampled.

Aging of valves from thin sections was effective for *Pleurobema collina*. The valves of this species are relatively small and thin and easily sectioned in ten to 35 min. Most annuli were easy to identify from the thin sections. Examination of six *P. collina* collected in 1989 (from the 23 marked in 1988) revealed that this species formed yearly primary growth rings. Neves and Moyer (1988) also demonstrated annual growth line formation in *P. oviforme*, *Medionidus conradicus* (Lea, 1834), *Villosa vanuxemensis* (Lea, 1838), and *Lasmigona subviridis* (Conrad, 1835) in southwestern Virginia.

The von Bertalanffy growth equation adequately described the growth of *Pleurobema collina* from the Johns and Dicks Creeks. The predicted values agreed well with observed values when N/age class was fairly large. For ages three to 15, the differences between predicted and observed values ranged from zero to 1.93 mm (N = 92), but for ages 16 to 19 (N = 8), the differences ranged from 1.11 to 4.09 mm.

The growth of *Pleurobema collina* is characteristic of other species of the subfamily Ambleminae. Members of Ambleminae usually have thick shells and grow slowly relative to thin-shelled species (Isely, 1914; Coker *et al.*, 1921; Coon *et al.*, 1977). Thick-shelled species grow most rapidly early in life, and later growth slows to a few mm/yr (Scruggs, 1960; Negus, 1966; Moyer, 1984). This is the pattern of growth in the James spinymussel; annual growth increment decreased steadily from 7.04 to 0.88 mm/yr with age.

There are several anthropogenic and natural threats to the James spinymussel's continued existence. Nearly all the riparian lands bordering streams with the James spinymussel are privately owned. With more intensive use of the land, it is probable that water quality and habitat suitability will deteriorate. At present, the most detrimental activities include road construction, cattle grazing, and feed lots that often introduce excessive silt and nutrients into the stream.

The introduced Asian clam [*Corbicula fluminea* (Müller, 1774)] is beginning to invade several sites where *P. collina* is found. This exotic bivalve is believed by many to be a threat to native unionids, especially in Atlantic coastal rivers (Fuller and Richardson, 1977; Kraemer, 1979; Clarke, 1986, 1988).

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Allometry of shell growth of caged and uncaged zebra mussels *(Dreissena polymorpha)* in Lake St. Clair

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Abstract. Growth and shell morphometrics of zebra mussels, *Dreissena polymorpha* (Pallas, 1771), were studied using caged and uncaged animals in Lake St. Clair. During unrestricted growth, mussels increased in length at about twice the rate as in height or width. Growth of mussels in cages was virtually isometric regarding shell length and width, but not so for length and height as well as for height and width. During growth from 4-20 mm, the L:W ratio was unchanged, the L:H ratio increased by 14%, and the H:W ratio decreased by 13%. In contrast, uncaged mussels, from either low or high density locations, showed strong allometry in terms of L:W ratio. L:W declined by approximately 25% during growth from 4-30 mm; L:H was isometric and H:W was allometric.

Zebra mussels reared in the smallest cage compartments had reduced shell dimensions, as well as weight, compared to individuals reared in large compartments. Weight was most strongly reduced (30.2%) followed by length (17.5%), width (15.7%), and height (11.4%). Crowding by up to ten individuals recruited from the outside did not significantly reduce the weight gain of caged mussels. Frequent sampling (12 times/yr) of caged zebra mussels did not affect final length, but significantly reduced weight gain and increased mortality, compared to infrequently sampled mussels (two times/yr).

The use of cages with individual compartments for *in situ* zebra mussel studies offers certain advantages, *i.e.* individuals are free of competition, predation, and other field complications due to crowding. However shell morphometrics are altered by such treatment. In general, final weights and lengths of zebra mussels in cages were comparable to both those achieved in uncaged animals and reported from European cage studies.

The invasive exotic bivalve, *Dreissena polymorpha* (Pallas, 1771) (zebra mussel) has, over the past five years, become a serious economic problem species in the Great Lakes and connecting waterways (Roberts, 1990; Nalepa and Schloesser, 1993). This invasion is also having ecological consequences, some of which have already been demonstrated (*e.g.* eradication of native species of unionid bivalves, Hunter and Bailey, 1992; Haag *et al.*, 1993), as well as others that are not fully documented (*e.g.* impacts on commercial and sports fisheries, Leach, 1993). Where densities are high, there are likely to be ecosystem level effects due to plankton removal and the attendant effects of water clarification and biodeposition of organic matter in the benthic sector.

Not all of the ecological impacts of zebra mussels are presumed to be negative. Biodeposition of filtered seston is likely to change surface sediments both quantitatively and qualitatively as this organic matter is colonized by microorganisms. Sediment enrichment is likely to have consequences for macrobenthic invertebrates with implications for a number of species higher in the food chain. Zebra mussels have a high caloric content and are a major food source for many species of fish and waterfowl (see Stanczykowska, 1977; French, 1993).

Despite extensive European literature on *Dreissena polymorpha*, North American studies are needed because of recently reported differences between the two populations. The majority of European ecological studies have been conducted on stable populations in marked contrast to the unusually high (and presumably unstable) densities that occur in many areas of the Great Lakes. Therefore, information on the biology and growth of the zebra mussel in the Great Lakes is important to understand its potential impact on native species, both in the benthic and planktonic sectors, including game and non-game fishes, invertebrates, and aquatic vegetation. Comparison of the parameters influencing growth in zebra mussels at different sites will help to identify reasons for their success in specific regions and the potential for their control by natural forces.

This study examined growth of zebra mussels reared in cages of different compartment sizes at two sites in Lake St. Clair: one near the Thames River (Ontario, Canada) and one near the Clinton River (Michigan, U. S. A.). Casual field observations had indicated that these two sites were markedly different in zebra mussel density in 1989 and 1990 (see distribution information in Hebert *et*

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al., 1991). Morphometric analysis of shell growth was included in these studies to evaluate the effect of crowding on shell proportions in mussels reared inside cages compared to those growing outside.

MATERIALS AND METHODS

CAGE DESIGN AND LOCATION

Overall design of the cage apparatus and details of compartment design are shown in Fig. 1. Cages were modified fish egg cages consisting of rectangular plexiglass plates with regularly spaced holes (S. J. Nichols, pers. comm.). The holes (compartments) were covered with plastic/fiberglass window screening of 1 mm^2 mesh and stocked with one animal per compartment. Cages were supported by a polyvinyl chloride (PVC) pipe anchored in a concrete pad which allowed their stable, upright position to be maintained on the lake bottom. The cages were positioned about 1.5 m under the water surface and about 0.5 m above the bottom. Zebra mussels of 3-5 mm initial length were used to stock all cages. Stock animals were measured using a microprojector that enlarged the image onto a graphics tablet, allowing measurements to be digitized and stored in a computer. Length (L), width (W), height (H), and weight measurements were collected according to the standards established for *Mytilus edulis* (Linné, 1758) by Seed (1968) and for zebra mussels by Stanczykowska (1964). Growth rates were calculated as differences between initial and final measurements divided by elapsed time in days.

Site locations are shown in Fig. 2. Most of the water mass at the Clinton River site consists of Lake Huron water from the north channel of the St. Clair River. Water volume contributed by the Clinton River is relatively minor due in part to the diversion of most of its flow to a canal approximately 13 km upstream from the study site. Zebra mussels have been present in the lower reaches of the Clinton River and in nearby areas since 1991 (Bitterman, pers. obs.).

The Thames River site in the southeastern part of Lake St. Clair consists of a different water mass than that at the Clinton River site. It is mostly Lake St. Clair water which is more stable and productive due to nutrient enrichment from Ontario rivers (Leach, 1991).

UNRESTRICTED GROWTH

Changes in shell dimensions during unrestricted growth (*i.e.* growth in uncrowded conditions) were evaluated using two different data sets. The first was pooled data from zebra mussels from both the Clinton and Thames River sites growing in cages that were of dimensions (26 mm diameter; 13 mm height) adequate to avoid physical inhibition of growth in any direction. Shell dimensions were expressed as ratios that were tested for deviation from

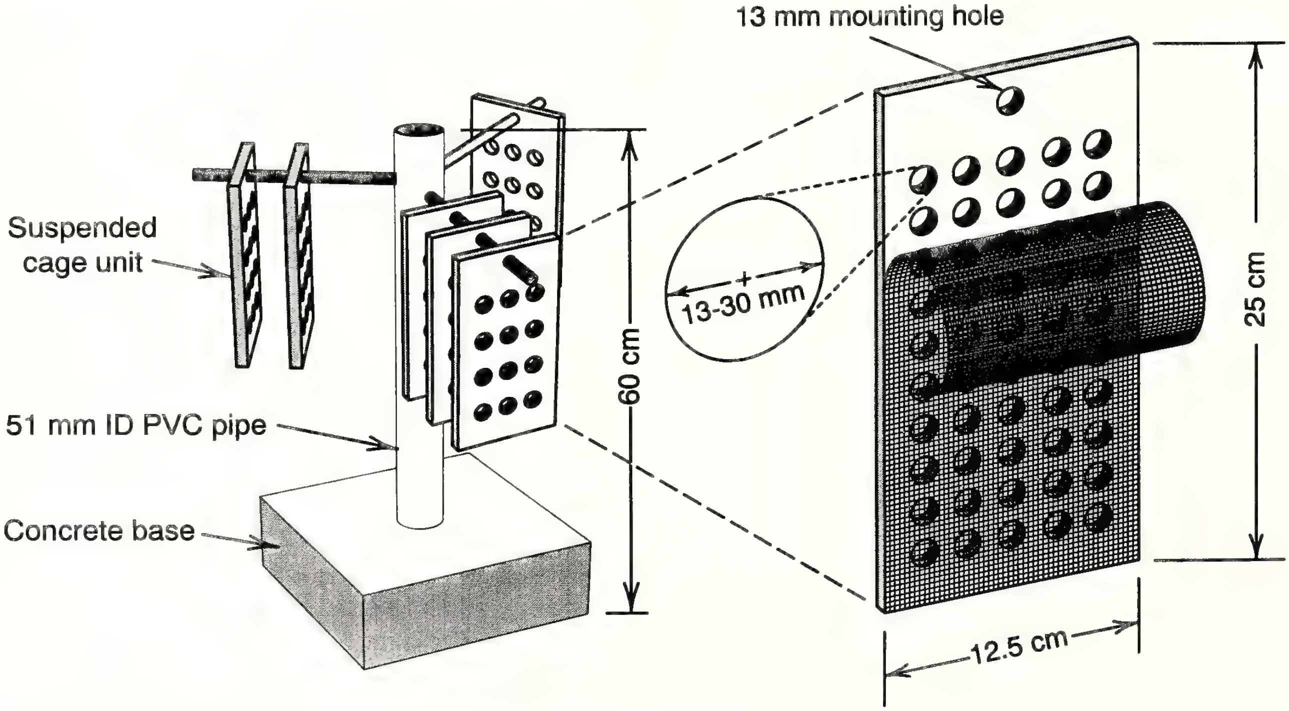

Fig. 1. Plexiglass cage units in which mussels were reared, showing the PVC support structure.

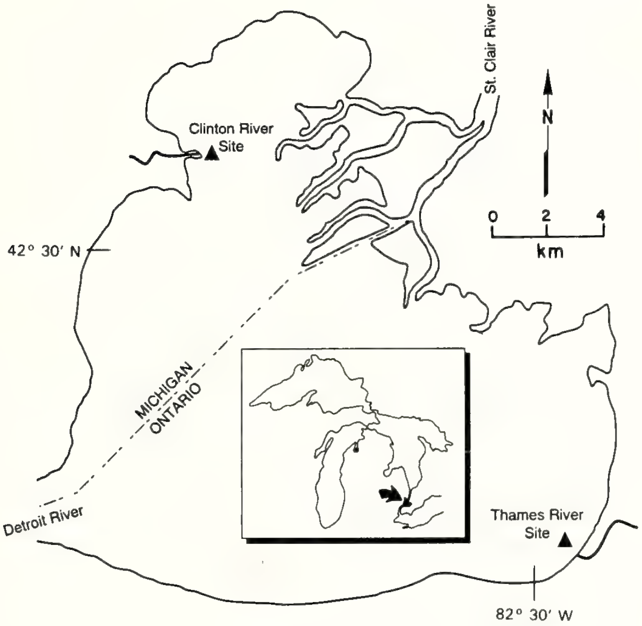

Fig. 2. Map of Lake St. Clair showing two sites where cages for zebra mussel growth studies were located.

zero slope by regression analysis. The second data set was obtained from animals in an area of Lake St. Clair that was sparsely populated (152/m^2; 26.1 mg whole wet weight/m^2) by zebra mussels. The site used was the "west" site of Hunter and Bailey (1992), located approximately 29 km due south of the Clinton River site. Here the primary substratum was shells of unionid bivalves.

RESTRICTED GROWTH

Changes in shell dimensions under restricted conditions were evaluated in cages and from field-collected material. Cage studies were of two types. In the first, cage units were set out at the two primary sites (Fig. 2). These cages initially consisted only of small compartments (13 mm diameter by 10 mm height; 1,327 mm^3) and were deployed from approximately mid-June 1990 to mid-May 1991. When it became apparent that zebra mussel growth rates were more rapid than anticipated and that shell length was being physically limited by compartment size, a subsample of the test animals was transferred to larger units measuring 26 mm diameter by 13 mm height (6,902 mm^3). Hence this 11-month study yielded data for mussels growing exclusively in small cages as well as for mussels started in small cages then transferred to large cages about three months into the study.

In the second cage study, four treatments (= cages) were set up at the Clinton River site, each consisting of a different compartment size having 20 animals per treatment. Diameter (mm), height (mm), and volume (mm^3) of the compartments were as follows: small = 13, 10, and 1,770; medium = 16, 13, and 3,485; large = 23, 13, and 7,201; and extra-large = 30, 15.6, and 14,702. Compartment dimensions were chosen to give an approximate doubling in volume with each larger size. The set of four cages was placed in the water on 18 May 1992 and retrieved on 9 September 1992 (114 days).

Both studies yielded growth data in terms of whole animal weight (shell plus soft tissue) and three shell dimensions. From the latter data, changes in shell proportions (allometry) during growth in restricted and unrestricted conditions were evaluated. The results of both studies were tested using analysis of variance (ANOVA) run on Statistical Programs for the Social Sciences/personal computer version (SPSS/PC+). The Tukey HSD (Honestly Significant Difference) multiple comparison test was used to identify which treatment(s) differed significantly from the others.

Field-collected mussels provided another means of evaluating the effect of physical restriction on shell proportions. Zebra mussels were collected from an area of Lake St. Clair ("east" site of Hunter and Bailey, 1992; 9.7 km northwest of the Thames River site) that was densely populated (11,655/m^2; 845.8 mg/m^2). These mussels were attached to the shells of dead unionids and to each other where they formed aggregations over the sediment surface.

EFFECTS OF INVADERS

Except in areas where natural recruitment is nil, most cage growth studies are subject to complications resulting from settling veligers and movement by small post-larval stages through the caging screen. The growth studies described above provided data on the effects that these "invader" mussels had on growth of the resident mussel. Because the initial size (4-5 mm length; 1.7-2.1 mm width) was only slightly larger than the maximum size mussel that could pass through the mesh, it was necessary to periodically examine the cages and remove invaders. Compartment-specific data on the number of invader zebra mussels at each sampling were kept for only the Thames River site. (The Clinton River site did not have this problem because there was virtually no recruitment of juveniles in either 1990 or 1991.) These data were matched with growth increments for the test mussels over the time interval since the previous sample. All invader mussels were removed during each shell and growth measurement.

GROWTH AND FREQUENCY OF SAMPLING

Growth studies at both Lake St. Clair sites were investigated with three cages (50 mussels each) on a frequently sampled schedule and an identical set of three on an infrequently sampled schedule. Frequently sampled mussels were retrieved, measured, and returned 12 times over 332 days, *i.e.* biweekly growth measurement in spring, summer, and fall of 1990, and monthly measurement in winter. Infrequent sampling involved only two measurements, initial and final, over the duration of the study. These schedules were maintained for the entire study period of 11 months, mid-June 1990 to mid-May 1991, and were repeated with newly stocked juveniles in 1991-1992. Measurement involved removal of the test mussels from their compartments for about 20 sec, and often–overnight transportation, during which the cages were held in aerated lake water at room temperature. In winter, the mussels were kept in ice-cooled water while in the lab. It was hypothesized that frequent sampling might reduce the growth rate and increase mortality compared to those on infrequent sampling schedules. Length and weight changes were tested using Fisher's Z where Z = the normal deviate (Zar, 1984). Between–treatment mortality was compared using the Student's t-test.

RESULTS

DIMENSIONAL CHANGES; UNRESTRICTED GROWTH

Data illustrating unrestricted growth of mussels in large cages are presented in Fig 3A. These mussels were stocked in the cages at an average length of 4.2 mm and were kept *in situ* for 332 days (July 1991 - June 1992) except for biweekly or monthly removal for measuring and weighing. Growth was rapid over the first 150 days (0.095 mm/day), then considerably slower over the next 182 days (0.015 mm/day) (Fig. 3A). Mean length attained at the end of the study was 21.2 mm, for an overall growth rate of 0.051 mm/day. Growth in width and height was about half that of length. For the first 150 days, width increased at an average rate of 0.042 mm/day, and height at 0.048 mm/day. Over the following 182 days, width increased at 0.010 mm/day and height at 0.007 mm/day. Overall average growth rates for width and height were identical at 0.025 mm/day.

Changes in ratios of shell measurements over this same period are shown in Fig. 3B. Isometric growth on this plot would be represented by a straight line with zero slope. Significant deviation from zero slope would be evidence for allometric growth. The ratio of length to width (L:W) remained constant over time (isometric growth) with the slope of the line not differing significantly from zero ($F_{(1,9)} = 2.484$; $P = 0.151$). In contrast, both the L:H and H:W relationships showed allometric growth with slopes that differed significantly from zero ($F_{(1,9)} = 55.846$; $P < 0.001$ and $F_{(1,10)} = 76.586$; $P < 0.001$). L:H increased over time from 1.80 to 2.06, whereas H:W decreased from 1.27 to 1.09. In other words, larger mussels reared in cages were somewhat lower in height relative to their length and width compared to juvenile mussels.

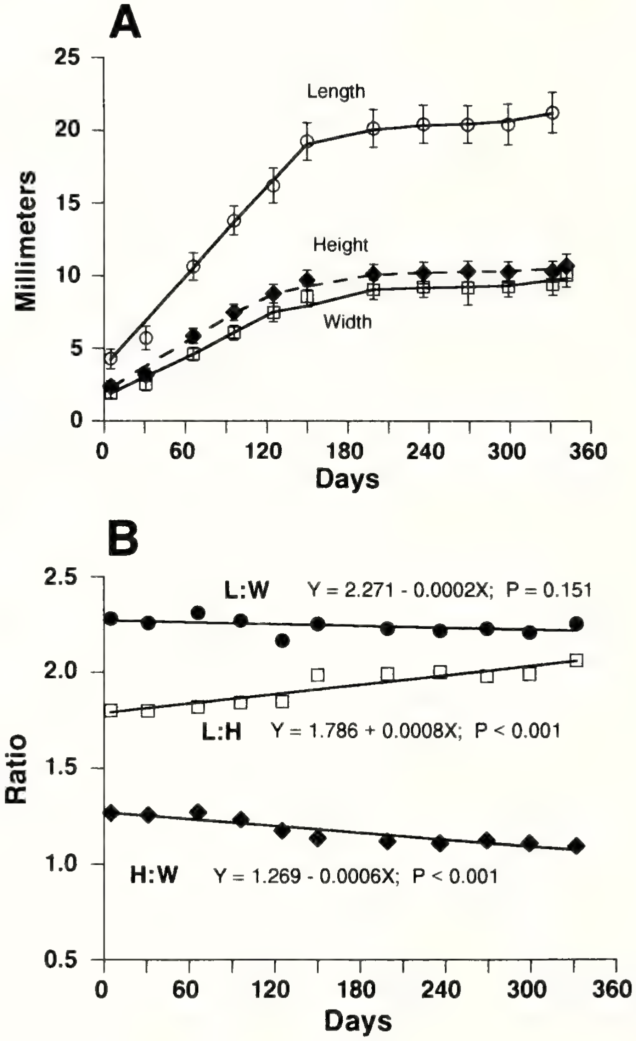

Fig. 3. A. Mean (± standard deviation) length, height, and width of zebra mussels reared in large (26 x 13 mm) cages at the Clinton River site from July 1991 to June 1992 (332 days). B. Changes in shell morphometrics during growth of the above mussels shown in terms of L:W, L:H, and H:W. Linear regression equations are given for each ratio with P values indicating whether the line has a slope significantly different from zero. Final sample size = 104 individuals.

Changes in shell proportions of uncaged zebra mussels are shown in Fig. 4. Fig. 4A shows shell ratios plotted in relation to length for the mussels at the low density site ($152/m^2$). Like the cage-reared mussels in Fig. 3B, those in Fig. 4A show allometric growth in terms of H:W (a valid comparison because growth in time and in length are highly correlated). However the other two ratios differ markedly with those of cage-reared mussels; L:W shows pronounced allometry whereas L:H does not. Fig. 4B illustrates shell

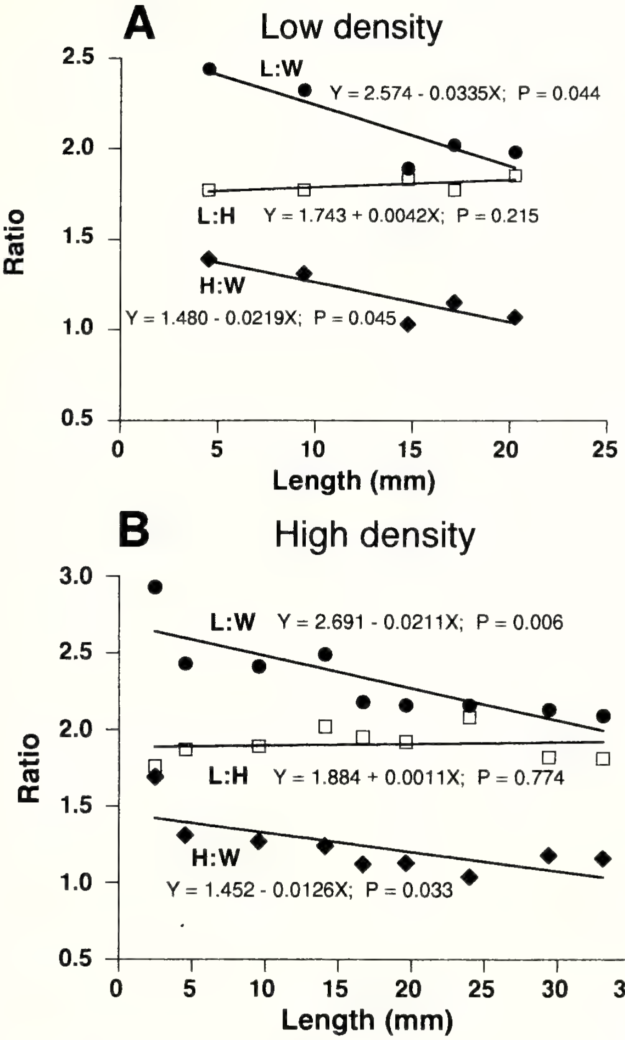

Fig. 4. A. Ratios of shell measurements versus shell length for uncaged zebra mussels from the low density site in southern Lake St. Clair in September 1990. Linear regression equations are given with P values for significance from zero slope. B. Shell ratios for a similar collection made at the high density site at the same time as A.

ratios during growth for mussels at the densely settled site (11,655/m^2). Despite a density difference of 75x, there was little difference between the high and low density groups in shell morphometrics during growth; L:W and H:W were allometric and L:H was isometric.

DIMENSIONAL CHANGES; RESTRICTED GROWTH

Compartment size study. Data from the 1990-1992 compartment size study at both the Clinton and Thames River sites showed that small size compartments restricted growth. Zebra mussels that were placed in small compartments then later transferred to larger compartments at the same site, grew faster and attained significantly larger size compared to those that remained in small cages (ANOVA, $F_{(59,42)} = 53.55$, $P < 0.001$). The two groups had similar initial mean weights (16 versus 19 mg) and mean lengths (4.4 versus 4.3 mm). However, by the end of the experiment, those reared in the small compartments had mean weights of 526 mg whereas those transferred to larger compartments weighed 936 mg, approximately 78% greater.

Growth under physical confinement not only reduced the final size and weight but also changed the mussel's shape by altering the proportions of length, width, and height. Compared to zebra mussels transferred to large cage compartments (26 x 13 mm), those remaining in small cage compartments (13 x 10 mm), had final lengths that were 18.6% smaller, final widths 23.0% smaller, and final heights that were 9.2% smaller. Hence these growth restricted mussels were proportionally taller than the less restricted group. Because their long axis was the first dimension to reach the physical limits of the compartment, it was not surprising that length was reduced in the small compartment animals. However, width showed an even greater growth restriction than length even though it was less directly constrained by compartmental dimensions.

In the second study, which tested the growth effects of four different compartment sizes, there were significant differences in the sizes of zebra mussels among treatments (Table 1). Although we attempted to set up each treatment with mussels of identical initial size, analysis showed small, but statistically significant, initial size differences among the four groups. Mean initial length of the mussels in the medium cages was significantly smaller than that of both the small and extra-large groups (ANOVA, $F_{(3, 236)} = 4.406$, $P < 0.005$; Tukey-HSD, $P < 0.05$) but not significantly different from that of the large group. Similar differences also existed for initial shell height and whole wet weight, but not for shell width (not significant).

These small initial differences were later obliterated by growth differences arising from compartment size effects, so that by the end of the experiment, growth in all dimensions was significantly less among the mussels in small compartments. Mean final length of animals in the small compartments was 12.3 mm whereas that in the other three compartments ranged from 14.1 to 14.9 mm (Table 1). This difference was significant (ANOVA, $F_{(3,186)} = 24.748$, $P < 0.001$; Tukey-HSD, $P < 0.05$). Similar differences, also significant, were observed in the final values of width, height, and weight. These differences in final shell dimensions and weight resulted in differences in relative growth (= raw change ÷ initial size). For example, gain in mean relative weight was 24x for small-compartment animals but 37x for large-compartment animals; similar differ-

Table 1. Initial and final measurements (mean ± standard deviation) and change in size of zebra mussels reared 114 days in cages with four different compartment sizes. Initial sample size was 60 for all cages. Final sample sizes were: small 51, medium 48, large 32, and extra-large 47. An * indicates the value is significantly different from the others in its measurement group (one-factor ANOVA, $P < 0.001$; Tukey-HSD, $P < 0.05$).

Compartment	Initial	Final	Change
	Length (mm)		
Small	4.43 ± 0.11	12.26 ± 0.60*	7.83*
Medium	4.10 ± 0.10	14.08 ± 1.21	9.99
Large	4.29 ± 0.11	14.38 ± 1.16	10.10
Extra-large	4.38 ± 0.09	14.86 ± 2.46	10.48
	Width (mm)		
Small	1.89 ± 0.12	5.86 ± 0.43*	3.98*
Medium	1.76 ± 0.11	6.46 ± 0.56	4.70
Large	1.83 ± 0.12	6.82 ± 0.50	4.99
Extra-large	1.86 ± 0.14	6.95 ± 0.75	5.09
	Height (mm)		
Small	2.31 ± 0.12	6.85 ± 0.55*	4.54*
Medium	2.13 ± 0.13	7.45 ± 0.60	5.32
Large	2.27 ± 0.11	7.53 ± 0.58	5.25
Extra-large	2.30 ± 0.10	7.73 ± 0.65	5.43
	Weight (mg)		
Small	16 ± 0.006	384 ± 0.07*	369*
Medium	13 ± 0.001	489 ± 0.13	477
Large	14 ± 0.006	511 ± 0.1	497
Extra-large	15 ± 0.006	551 ± 0.1	535

ences were observed for width and height.

Final size of the mussels was correlated with compartment size even though this was not the case initially (Table 1). Mussels in the small, medium, large, and extra-large compartments had mean length increments of 7.83, 9.99, 10.10, and 10.48 mm, respectively. Mean final length of mussels in the small compartments was significantly less than that in the other size compartments (ANOVA, $F_{(3,194)} = 4.66$, $P < 0.003$). The other dimensions (width, height, and weight) followed similar patterns (Table 1). Even though mussels stocked in the small cages were initially largest (4.43 mm length), they were smallest at the end of the experiment (12.26 mm). Differences in initial size were negligible in relation to growth differences resulting from the effects of compartment size.

Considerable growth restriction experienced by mussels in the small compartments and minor growth restrictions experienced in other compartments are shown as a three-dimensional plot in Fig. 5. Mean raw change of length, width, and height were proportional to compartment size, and mussels in the small compartments had by far the smallest dimensions of the four groups. In contrast, there was relatively little size difference among mussels in the medium, large, and extra-large treatments.

Mean weight also increased with compartment size. The mean weight increments were 369, 477, 497, and 535 mg for the small through extra-large compartments, respectively. Once again, the mussels in small compartments had mean weight increments that were significantly less than those for mussels reared in the other three compartment sizes (ANOVA, $F_{(3,194)} = 5.83$, $P < 0.001$).

Invaders. A recurring problem at the Thames River site was the tendency for uncaged juvenile mussels to invade the cage compartments, creating potential crowding of the test mussels. In some cases there were as many as eight invading mussels in one compartment. However, invaders apparently did not decrease the growth of the caged zebra mussels. Relative weight gain in test mussels varied considerably, but there was no indication of any systematic weight reduction or change associated with increased number of invaders. The correlation between relative weight gain of the resident mussels and number of invader mussels was not only low (correlation coefficient, $r = 0.103$) but not significant ($P = 0.792$). The same pattern was observed for relative length of test mussels when compared to the number of invaders.

Growth and sampling frequency. A comparison of changes in length and weight was made between caged mussels that were sampled frequently and infrequently.

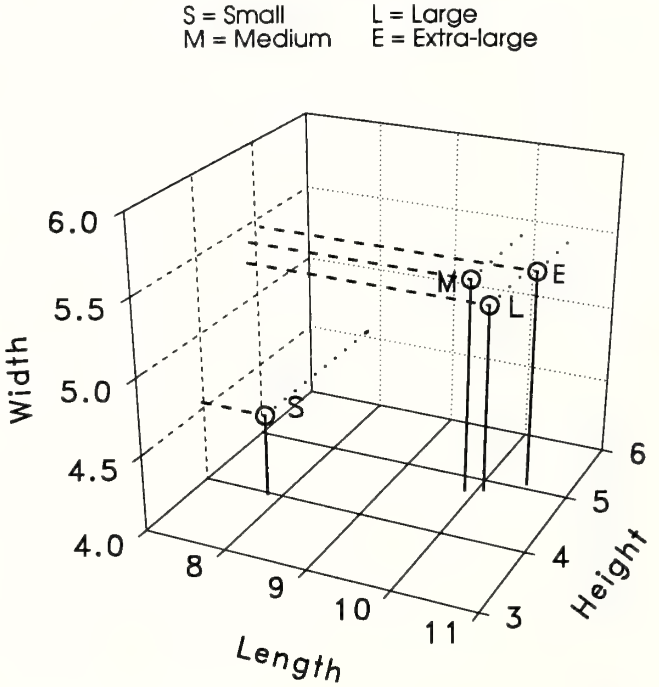

Fig. 5. Three dimensional plot of mean relative change in length, width, and height of zebra mussels reared in cages with four compartment sizes at the Clinton River site from May-September 1992.

The former group, with an initial mean of 4.27 mm, grew to 21.23 mm for an increase of 16.96 mm, whereas the latter group grew from 4.12 mm initially to 21.50 mm, for an increase of 17.38 mm. These two groups were not significantly different in length increase ($Z = 1.602$, $P > 0.05$). In contrast, frequently sampled mussels had significantly lower whole wet weight at the end of the experiment (frequent = 1.377 g, infrequent = 1.455 g; $Z = 2.163$, $P < 0.05$). Disturbance and trauma resulting from sampling appear to have a measurable impact on growth in weight.

Mortality rates were also affected by sampling. Animals measured infrequently during the study had significantly lower mortality than those animals measured frequently indicating that removal and handling were detrimental to survival (t-Test, $t_{(0.05,11)} = 4.202$, $P = 0.002$). Infrequently measured Clinton River site animals had a mortality rate of 16.7% in 1990-1991, whereas frequently measured animals at the same site had a rate of 30.0%. The Thames River site in 1990-1991 showed a mortality rate of 17.1% for infrequently measured animals and a rate of 24.7% for those measured frequently. Similar results were again observed in the subsequent year. The Clinton River site had a mortality of 18.0% for frequently measured animals and only 9.8% for those infrequently measured. The Thames River site also had an 18.0% mortality rate for frequently measured animals, but only 7.1% for those measured infrequently.

DISCUSSION

These studies demonstrate that growth of individual zebra mussels can be studied *in situ* under relatively uniform conditions using cages built of non-toxic materials. Individuals can be housed in cylindrical compartments with screening over each end. Cages of this design are relatively inexpensive and allow easy access to the animals for measurement or manipulation over the course of the experiment. It is clear that the compartment dimensions must be of adequate size to not restrict growth in any dimension. In our Lake St. Clair field studies, animals started in June 1991, at a mean length of 4.2 mm (17 mg wet weight) attained a length of 18-19 mm by the end of October and a length of 20-21 mm (110-130 mg) by May of the next year (Bitterman, 1992). Field data showed that not all growing seasons produced "good" growth, an observation that has been made by several other workers (see Dorgelo, 1993, and references therein). Annual and between-site variations in the growth of cage-reared zebra mussels will be more fully examined in a future report.

Growth of caged zebra mussels in isolation obviously differs somewhat from growth under more natural (usually crowded) conditions, where each mussel in a dense cluster is subject to strong intraspecific competition in the form of physical pressures from direct contact and collective growth of adjacent mussels. However, the advantage to cage studies is that growth can be evaluated without confounding effects of intraspecific competition, predation, or the more subtle effects of crowding. There is also the added advantage of being able to unambiguously monitor the growth of single individuals without needing to mark them. Previous studies have used cages to monitor growth, however, these have involved groups of mussels in each cage (Smit *et al.*, 1992; Dorgelo, 1993). The effect of cage-rearing on ratios of shell measurements observed in this study is one example of a difference arising from rearing in isolation. Width tended to be isometric with length among caged animals in contrast to uncaged animals which were not isometric. Allometric growth in length and width was observed in uncaged mussels regardless of density, suggesting that normal crowding has little impact on shell morphometrics. Based on field observations, it appears that year-to-year variations in lake conditions also exert a measurable influence on relative growth with consequences for allometry.

It has been asserted that morphometric features of zebra mussel shells vary only slightly among different lakes with no significant difference between lakes (Stanczykowska, 1964). In a survey of 11 Polish lakes, zebra mussels had L:W ratios with a mean of 2.24 in first-year mussels to 1.85 in five-year mussels. L:W ratios decreased with age at all sites. In contrast, L:H ratios increased with age from 1.93 in the first year to 2.06 in year five (Stanczykowska, 1977). Our L:W ratios are very similar to those reported by Stanczykowska, with mussels of 4 mm length having an initial L:W ratio of 2.4, decreasing to 1.8 for mussels of 20 mm length. L:H ratios reported here for Lake St. Clair ranged from 1.7 to 1.9. The main difference is that our data are for a single calendar year whereas Stanczykowska's data are for growth over five years. Such differences illustrate the influence of slower growth rates and longer time to maturity on allometry of growth in stable European populations in contrast to faster growth rates of recently invasive North American populations.

Our data suggest that field density differences of the magnitude reported here have little or no consequences for shell growth morphometrics. However, growth occurring under caged conditions altered shell dimensions enough to change allometry to isometry and vice versa. Based on our cage study in Lake St. Clair, compartments of 30 mm diameter and 15 mm height are recommended as adequate for growth studies up to one year. Longer studies, especially under optimal growth conditions, may require larger compartments. In Lake St. Clair, the occurrence of zebra mussels over 30 mm is not unusual, however such animals normally constitute a relatively small percentage of the population. In contrast, compartments of only 13 mm diameter markedly reduced the length and weight attained by test mussels compared to those in larger compartments even after only 114 days. Additionally, such growth-restricted mussels had different proportions of shell length, width, and height compared to uncaged mussels. Zebra mussels reared in intermediate size compartments showed only slight reduction in their length compared to animals in extra-large compartments. Although the differences were not significant, they suggest that cage-reared mussels may be responding to decreasing compartment space before they reach the absolute physical cage limits.

Observed growth differences probably would have been greater had our study extended beyond 114 days. Our long-term cage studies used compartments of 26 mm diameter and 13 mm height, which yielded a mean maximum length of 20.8 mm over 336 days in 1991-1992 (a "good" growth year) and a mean maximum length of 16.6 mm over 343 days in 1990-1991 (a relatively poor growth year) (Bitterman, 1992, and unpublished data). Mean annual length and weight increments were 14.3 mm and 882 mg for 1990-1991, and 18.87 mm and 1540 mg for 1991-1992. Relatively large annual variation in growth may explain why rates reported in the North American literature are so divergent. For example, Hebert *et al.* (1989) reported Lake St. Clair zebra mussels grew at a rate of 10 mm/yr whereas Mackie (1991) found that most individuals in the same lake grew 15-20 mm/yr.

Our overall growth rates for unrestricted cage-reared mussels (18.6 mm/yr, 0.051 mm/day) are comparable to those reported for European lakes. Dorgelo (1993) reported zebra mussel growth with a mean of 0.54-0.59 mm/wk (= 0.077-0.084 mm/day) for a Dutch oligotrophic lake, and ca. 0.050 mm/day for a mesooligotrophic lake. A Rhine River population with initial sizes of 4-7 mm grew at 14 mm/yr with virtually no net growth in winter (Neumann *et al.*, 1993). Smit *et al.* (1992) reported growth rates for several Dutch lakes, including Lake IJsselmeer, where zebra mussels initially 4.2 mm added 12.35 mm in one growing season.

Zebra mussel growth rates are similar to those of the Asiatic clam, *Corbicula fluminea* (Müller, 1774), but greater than those of the sphaeroidean clam, *Pisidium casertanum* (Poli, 1791). *C. fluminea* had a mean growth rate of 0.045-0.080 mm/day or 16-30 mm/yr (Aldridge and McMahon, 1978) and *P. casertanum* had a mean growth rate of 0.011 mm/day or 4 mm/yr (Mackie and Rooke, 1983). *C. fluminea* is an exotic clam from Asia and *P. casertanum* is one of many sphaeroidean clams native to American freshwaters that are of comparable size to zebra mussels. These growth rate differences are consistent with maximum size differences among these three species.

In the restricted growth experiment, the small compartments had a pronounced effect on zebra mussel growth, especially length, because that dimension was physically the most directly limited. Growth in width and height were not as constrained. Length of mussels in small compartments was reduced by 17.5% compared to that in extra-large compartments. Similar reductions occurred in width (15.7%) and height (11.4%). This flexibility in growth form is likely to be an adaptation to colonial life. Colonies can consist of tens to thousands of individuals of all age classes (Lewandowski, 1976). Densities in Mazurian Lakes have been recorded from 100-1000 individuals/m^2. Lake St. Clair had densities as high as 200,000 individuals/m^2 (Mackie, 1991). Older mussels tend to be directly attached to the substratum, often toward the center of the cluster, and covered by individuals of decreasing age toward the outer edge of the cluster. Other biofouling macroinvertebrates, such as barnacles, are known to change the dimensions of their growth due to the physical interference of crowding rather than differential exploitation of food or other resources (Connell, 1961). However, we saw no evidence in our study for lateral compression of the magnitude commonly observed in dense aggregations of barnacles or the marine mussel *Mytilus edulis.* Seed (1968) suggested that shell morphology in *M. edulis* was influenced by density and growth rate. Physical compression, which is greatest in areas of fast growth and high density, leads to elongated growth form; whereas low density populations with low compression have shells that tend to be higher (more triangular) in relation to length.

Invading zebra mussels did not have a negative effect on test mussels in cages. This may be due to the aggregating life-habit in which zebra mussels naturally occur, making them relatively tolerant of crowding. Lewandowski (1976) observed that larvae settled more frequently on live zebra mussels than on empty shells or pebbles. He stated that adults exert an attractive force on the settling mussels.

The interactions between zebra mussels in aggregations may be beneficial. For example, the irregular surfaces of mussel clusters create eddies increasing the amount of particulate food available (Frechette *et al.*, 1989). Conversely, life as part of a dense aggregation of mussels causes damage to some individuals. In Polish populations growth rates and maximum age decreased from overcrowding (Stanczykowska, 1964). Both Wiktor (1963) and Stanczykowska (1977) found that individuals in the bottom layers of clusters had more deformations, attributed to the constant squeeze of neighboring mussels. Not only were the morphological features changed, but the caloric value of the dry body weight of the mollusks decreased as the density of the colony increased. As the population density increased, the body condition deteriorated. It was also noted that zebra mussels in dense populations consumed less food than those living in areas of lower mussel density (Stanczykowska, 1977). Hunter and Bailey (1992) observed elevated shell:tissue ratios and reduced zebra mussel condition when crowded. In large individuals (20-30 mm length) from sparse populations, tissue mass was high in relation to shell mass yielding a low shell:tissue ratio of 9.5:1. In contrast, similarly sized individuals from crowded populations had shell:tissue ratios averaging 15.5:1.

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Early development of the estuarine mollusk *Polymesoda solida* (Philippi, 1846) (Bivalvia: Corbiculidae) in Lake Maracaibo, Venezuela

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Abstract. The estuarine clam, *Polymesoda solida* (Philippi, 1846), from Lake Maracaibo, Venezuela, was spawned and reared under laboratory conditions to monitor its early development. Spawning was induced via salinity changes and serotonin injections. Serotonin injections were more effective than salinity changes yielding viable gametes in 64% of the specimens used. Eggs and sperm were released into the water and fertilization was achieved by mixing 5 ml of eggs with 1 ml of sperm. After fertilization, the first two embryonic divisions occurred at 1 and 1.5 hr, trochophore larvae appeared between 24 and 30 hr, and free swimming straight-hinge veligers developed two days after the trochophores. Umbo stages with limited movement were seen after the fifth day. Trochophore and straight-hinged veliger stages were observed surviving inside the gelatinous envelope that surrounds the eggs. This envelope dissolved in most cases when the trochophore stage was reached, but persisted in those experiments where the culture environment deteriorated. We postulate that this envelope plays an important role in protecting the early developmental stages under adverse conditions.

For more than a century the existence of the estuarine bivalve *Polymesoda solida* in Lake Maracaibo, Venezuela (Fig. 1), has been known. This mollusk was believed, for more than 120 years, to be an endemic of this lake (Deshayes, 1854; Prime, 1865; Ten Broek, 1950; Rodriguez, 1973), but Cosel (1977) and García (1984) showed that populations of this species live in the Orinoco River delta in northeastern Venezuela and in coastal lagoons on the northeast Atlantic coast of Colombia. None of the published literature has described the eggs and larval development (García, 1984; Severeyn *et al.*, 1986, Severeyn, 1988, 1993). We describe here the development of *P. solida.*

TAXONOMY

Severeyn (1993) reviewed the status of *Polymesoda* species and considered *P. arctata* (Deshayes, 1854) from Lake Maracaibo a synonym of *P. solida* from the Atlantic coast of Nicaragua. The geographic range of *P. solida* therefore extends from the Orinoco River, Venezuela, to Gales Point, Belize (Severeyn, 1993). Within this range, four populations of *P. solida* have been described as different species.

Species described as *Polymesoda arctata* from Venezuela, *P. regalis* (Prime, 1865) from Colombia, *P. acuta* (Prime, 1861), *P. ordinaria* (Prime, 1865), and *P. boliviana* (Clessin, 1879) from unknown localities on the Atlantic side of Central America are all *P. solida.* Samples of *P. germana* (Prime, 1870) from Tampico, Veracruz state,

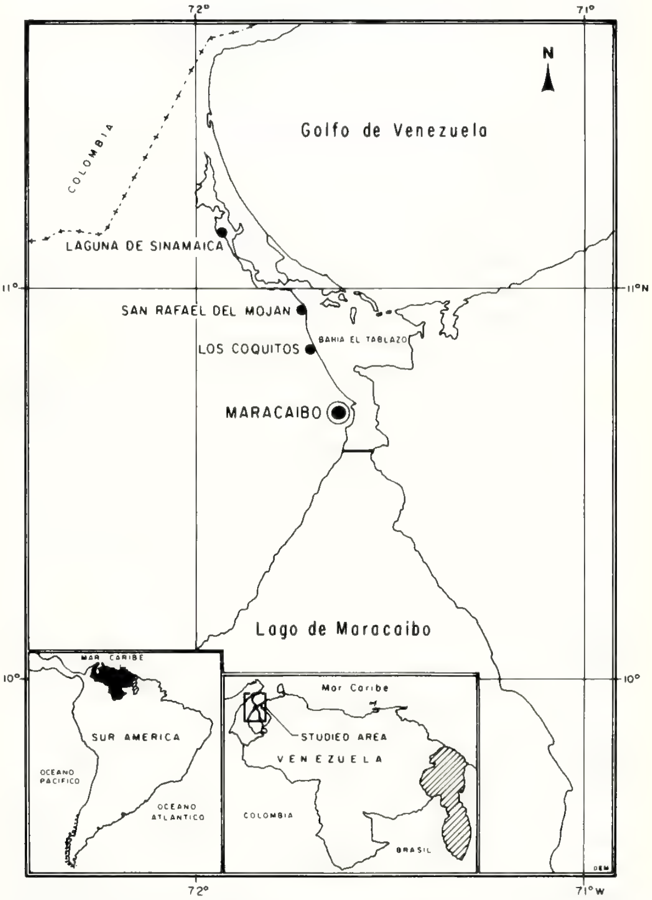

Fig. 1. Area of study indicating collection stations at Los Coquitos and San Rafael del Moján.

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Mexico, were *P. solida*, but Severeyn (1993) considered the locality recorded doubtful because recent collections in the same locality have not found specimens. We follow Severeyn (1993) in adopting *P. solida* as the valid name for the species found along Venezuelan coasts.

OBJECTIVE AND SIGNIFICANCE

The density of *Polymesoda solida* populations in Lake Maracaibo (up to 200 specimens/m^2) (Rodriguez, 1973) has made it an important source of human food. Its exploitation grew quickly in the late 1970's, and dense populations in Laguna Sinamaica (Fig. 1) were depleted (Severeyn *et al.*, 1986). Presently, at least 25,000 kilograms (whole weight including shells) are consumed monthly in the capital of Venezuela. The use of *P. solida* as food from underexploited areas will increase because populations of other marine species (*e.g. Tivela* and *Donax*) are now depleted after more than 30 years of commercial harvest.

Despite a geographic range covering nine countries (Severeyn, 1993), *Polymesoda solida* has not been studied except for the population in the Lake Maracaibo, Venezuela, and the isolated report of Cosel (1977) in Colombian coastal lagoons.

METHODS

COLLECTION OF SPECIMENS

The specimens of *Polymesoda solida* used in this study were collected between May and July 1985, from two stations, Los Coquitos and San Rafael del Moján, on the northwestern coast of the Maracaibo Straits (Fig. 1). Salinities at collection sites varied from three to nine ppt.

All specimens were collected in each of ten, 40 x 40 cm quadrats, five meters apart, along a transect parallel to the low tide water line. Each collection consisted of removing the sediment to five cm deep, and sieving it through a two mm mesh. Sediment was mostly coarse to medium sand with 1-3% clay.

Specimens larger than 25 mm were brought to the laboratory in plastic containers containing aerated water from the place of collection. This was done because there is evidence that *Polymesoda solida*, which reaches sexual maturity at 20 mm (Severeyn *et al.*, 1986; Severeyn, 1988) may initiate spawning with a change in temperature, salinity, or other conditions.

LABORATORY PROCEDURES

In the laboratory, the clams were placed in 30 l glass aquaria containing sediment and filtered water from the collecting locality. These closed systems were aerated, with the salinity maintained at 5 ± 1 ppt and temperature at 27 ± 1° C. After one week of acclimation, animals were selected for spawning.

SPAWNING AND LARVAL DEVELOPMENT

Different techniques to provoke spawning under laboratory conditions have been tested in *Polymesoda solida* (see García, 1984). These included sudden changes in salinity and temperature, mechanical stress (strikes), desiccation, and chemical stress (pH changes, KCl and serotonin injections). Only salinity changes and serotonin injections have been successful. The use of these techniques in *P. solida* was described by García (1984), Severeyn *et al.* (1986), and Ewald *et al.* (1986). Gibbons and Castagna (1984) originally described in detail the serotonin technique used for spawning induction in *Mercenaria*. Our experiments consisted of dropping or raising the salinity in the aquaria from that at the collection site to 0 or 35 ppt, respectively. These changes were always sudden.

The rearing of embryos and larval stages followed the standard techniques of Loosanoff and Davis (1963). Embryos and larval stages were kept in 100 ml glass aquaria placed into environmentally controlled cabinets (Percival Co., Model I-35LL). Temperature was maintained at 26 ± 1° C, and salinity at 5 ± 1 ppt. A cycle of 12 hr darkness and 12 hr light simulated a natural daily cycle. After the trochophore stage was reached, bacterial contamination was controlled by adding five drops of Rifampicin (0.1 g/l) every two days to the 100 ml aquarium.

FEEDING OF LARVAL STAGES

Axenic algal cultures were used as food sources for veliger stages. The algae included two unidentified flagellate species and *Skeletonema* sp. isolated from Lake Maracaibo waters, and *Isochrysis galbana* Parke obtained from Rosenstiel School of Marine and Atmospheric Sciences in Coral Gables, Florida. Local algal clones are part of the permanent collection of our laboratory and were isolated by the dilution technique in agar-agar Petri plates enriched with f/2 nutrient medium (Guillard and Ryther, 1962). Ten ml of algal concentrate, from a 30 l mass culture, was added every two days to the aquaria containing 100-150 trochophore larvae. Every two days, five ml of the same algal concentrate was added to less densely populated aquaria containing 15-20 veliger larvae. Before each addition of algae concentrate, water and detritus were removed and replaced with sterilized water of the same salinity, prepared with Instant Ocean (Aquarium Systems, Eastlake, Ohio).

RESULTS

SPAWNING AND FERTILIZATION

Table 1 shows the results of those experiments that produced successful spawning of *Polymesoda solida.* Under our conditions, salinity change was not as successful as the use of serotonin for spawning induction. The four experiments that employed this chemical were successful in producing viable eggs and sperm. All other methods caused the production of large, hose-like packages of eggs from females (Fig. 2A) and balls of radially arranged spermatozoa from males, oriented with their heads toward the center (Fig. 2B).

The numbers of males and females that spawned were similar, slightly favoring females (55%). Almost 65% of the animals treated with serotonin spawned. Only specimens from Los Coquitos responded to the serotonin.

Spermatozoa of *Polymesoda solida* have a long, cuneiform head with a mean length of 5 µm and a maximum width of 2 µm. They possess a flagellum about 50 µm long. Eggs are completely spherical at spawning with a mean diameter of 60 µm. They are enclosed in a gelatinous envelope (King *et al.*, 1986), called a hyaline capsule by Severeyn (1993), that increases their effective diameter to 120 µm (Fig. 3A, hc).

Obtaining fertilized eggs was no problem. Nearly 100% of the eggs were fertilized using the techniques suggested by Loosanoff and Davis (1963). Unfertilized eggs in each experiment were removed to decrease the chance of bacterial contamination.

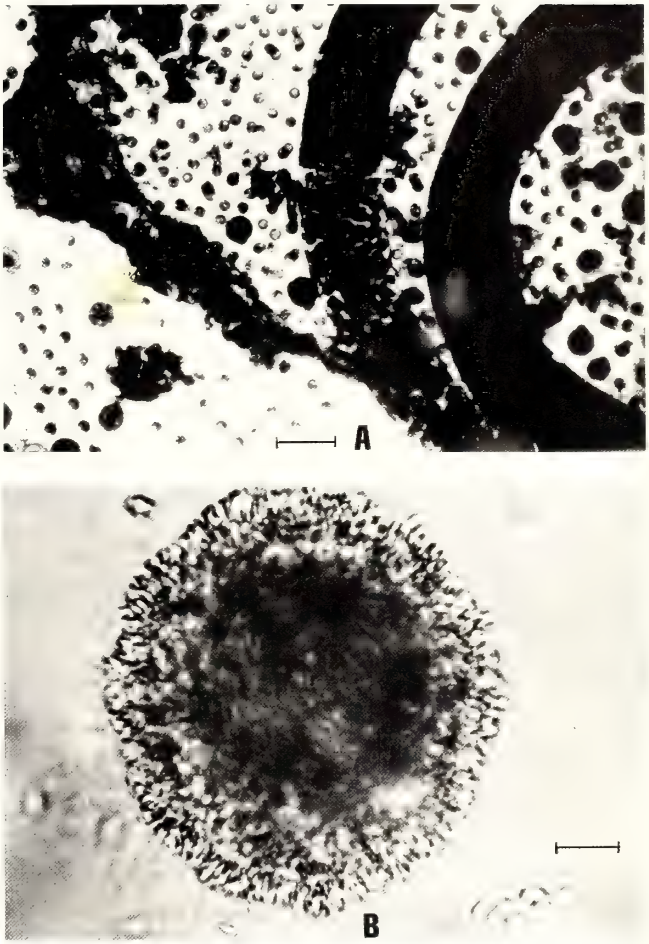

Fig. 2. Abortive stages in *Polymesoda solida.* A) Female hose-like packages (scale bar = 120 µm). B) Male ball of sperm (scale bar = 25 µm).

EARLY CELL DIVISION AND LARVAL DEVELOPMENT

Table 2 shows the developmental times (with maxima and minima) for all stages. Fertilization was recognized by the appearance of a thick fertilization membrane (Fig. 3A, fm). Ten to 30 min later, a polar body appeared. One and a half hr after fertilization, the first cleavage occurred (Fig. 3B). The second and third cleavages occurred 30 min and less than two hr after fertilization, respectively. Five to 8 hr after fertilization, most embryos were in blastula or gastrula stages. Trochophore larvae (Fig. 4A) were observed 24-36 hr after fertilization and straight-hinged veligers (Fig. 4B) were present after the second day. The few veligers that developed to the umbo stage appeared about five days after fertilization. The size of the two-day straight-hinged veliger varied from 137.5-176.0 µm and that of the few umbo stages observed between 270-290 µm.

Despite the fact that both temperature and salinity were maintained, some embryos developed quickly and others slowly. The mortality of embryos prior to the trochophore stage (Fig. 4A) was low (5%), but then increased rapidly. A 70% mortality rate was observed at the trochophore stage, and only 5-7% of the embryos reached the straight-hinged veliger stage (Fig. 4B). Only 0.04% of the embryos reached the umbo stage.

Table 1. Results of the experiments of spawning induction in *Polymesoda solida* (F, female; FT, free trochophore; M, male; MSR, maximum stage reached; SHV, straight-hinged veliger).

Exp.	Treatment	N	Spawned	M	F	MSR
1	Sal. changes	25	3	2	1	SHV
2	Sal. changes	25	2	1	1	VEL
3	Serotonin	40	31	11	20	FT
4	Serotonin	16	12	7	5	SHV
5	Serotonin	20	6	4	2	Umbo
6	Serotonin	9	6	2	4	SHV
Total		135	60	27	33	
Percent			44%	45%	55%	

Table 2. Development times after fertilization of embrionic and larval stages of *Polymesoda solida* under laboratory conditions. (*, capsule-free. Encapsulated trochophores appeared as early as 12 hr after fertilization).

Stage	Mean Time	Range
Polar body	20 min	10-30 min
1st cleavage	60 min	45-85 min
2nd cleavage	90 min	70-110 min
Gastrula	5 hr	3-7 hr
Blastula	7 hr	4-9 hr
Trochophore*	30 hr	14-42 hr
Straight-hinged veliger	48 hr	36-68 hr
Veliger (umbo)	5 d	4-7 d

DISCUSSION

SPAWNING

The percentage of animals that spawned after treatment with serotonin (64.7%) was higher than those obtained by Gibbons and Castagna [1984; 45% in *Geukensia demissa* (Dillwyn, 1817) and 42% in *Mercenaria mercenaria* (Linné, 1758)]. However, the small number of spawning specimens (44.4%) suggests that most specimens were not ready for spawning despite the fact that they were collected during the spawning season. Severeyn (1988) demonstrated that *Polymesoda solida* has two spawning periods during the year, one between April and June and the other between November and January. We agree with Chanley (1975) who indicated that gonadal stage is a key factor controlling the possibility of spawning and the production of viable gametes under laboratory conditions, but these results suggest that the effectiveness of serotonin in inducing spawning is limited.

The amount of sperm released by *Polymesoda solida*, 6.68 x 10^6 cells/ml/spawning event, was similar to the sperm density observed in *Corbicula fluminea* (Müller, 1774) (7.7 x 10^6 cells/ml/spawning; King *et al.*, 1986). However, the number of eggs released by *P. solida* was larger than that observed in *Corbicula*. The fecundity of *P. solida* females was nearly 5000 eggs/100 ml/spawning while *Corbicula* only spawned seven eggs/500 ml. This difference is clearly in response to different reproductive strategies.

THE GELATINOUS ENVELOPE

A feature of *Polymesoda solida* eggs that needs special comment is the presence of a hyaline capsule (Fig. 3A, hc). This capsule is present from the time eggs are liberated and normally disappears after the trochophore stage is reached. Occasionally, we observed that it remained as the trochophore developed, and sometimes through more advanced larval stages. Straight-hinged stages, actively moving within the capsule up to a month after fertilization, were observed. We considered these encapsulated larval stages anomalous.

The role of the capsule is controversial. Severeyn (1993) argued that it could play an important role in protecting the eggs and in their ability to disperse within and between estuarine areas. Similar capsules are quite common in the Corbiculoidea (Corbiculidae and Sphaeriidae) and Unionoidea (Mackie, 1984). Severeyn (1993) verified its presence in four species of *Polymesoda*. Olsen (1976) reported it in *P. caroliniana* (Bosc, 1801). King *et al.* (1986) also found it in North American *Corbicula fluminea* and although it was not mentioned by Morton (1989) in *P. erosa* (Solander, 1786) (= *P. coaxans* Rumph, 1741) it is evident in some of his figures. Considering our rearing conditions, we hypothesize that this capsule may protect advanced larval stages as long as unfavorable environmen-

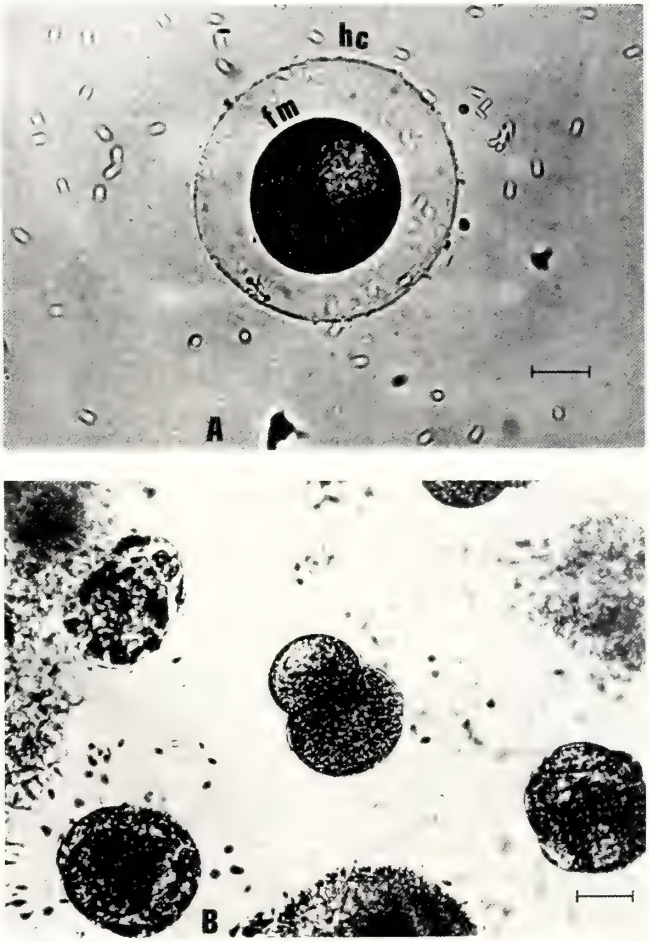

Fig. 3. Early embrionic stages of *Polymesoda solida.* A) Recently fertilized egg showing the fertilization membrane (fm) and the hyaline capsule (hc) (scale bar = 25 µm). B) First cleavage (two-celled embryo) (scale bar = 25 µm).

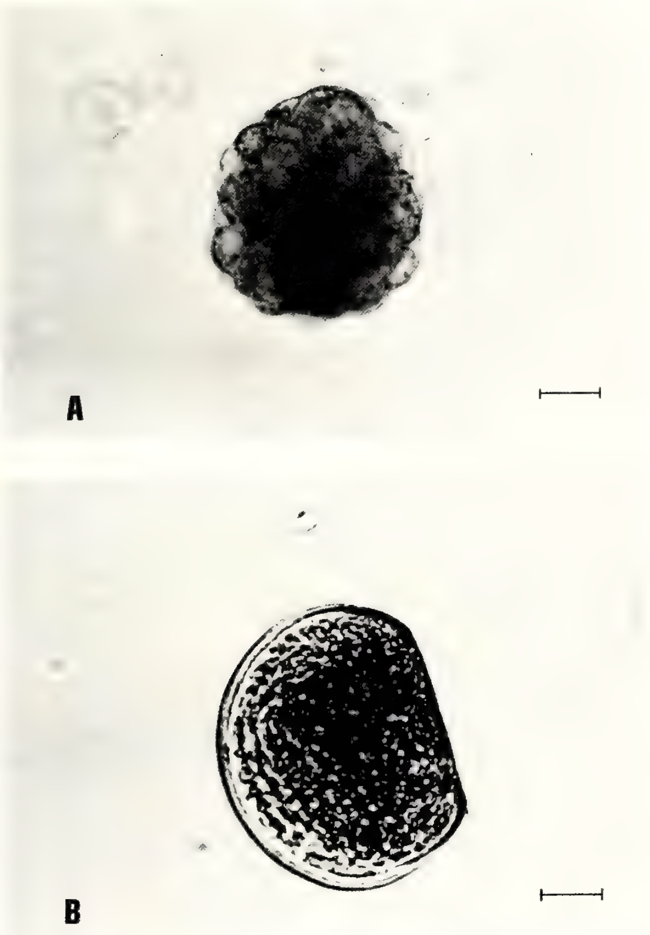

Fig. 4. Larval stages of *Polymesoda solida.* A) Trochophore larva (scale bar = 25 µm). B) Straight-hinged veliger (scale bar = 35 µm).

tal conditions persist. This coincides with observations made by Olsen (1976) who remarked that in *P. caroliniana* the hyaline capsules disappeared after fertilization, leaving embryonic and larval stages capsule-free. However in some cases, the capsule remained until the trochophore stage was reached.

Further research is needed to clarify the nature and function of the hyaline capsule.

DEVELOPMENT

The results suggest that *Polymesoda solida* has a larval planktonic cycle that could be as short as five days, likely reaching the umbo stage in one week. Metamorphosis of *P. solida* was not successful under our laboratory conditions but we believe that bacterial contamination and subsequent mortalities were important factors constraining this final phase of the larval cycle. In a few cases we observed umbo-stage individuals displaying crawling behavior, therefore assumed to be very close to reaching metamorphosis. We suspect that unfavorable conditions (*e.g.* unsuitable substratum, bacterial contamination, inadequate salinity, etc.) may extend this seven-day cycle at least as long as one month. Apparently, the presence of the hyaline capsule allows this cycle extension.

These results are based upon laboratory experiments and may not necessarily reflect the natural situation. The broad variation of developmental times for the encapsulated trochophore, the capsule-free trochophore and the straight-hinged veliger stages suggests that these stages may be particularly sensitive to environmental changes.

The developmental mean times observed in *Polymesoda solida* (Table 2) differ from those reported for *P. caroliniana* and *Corbicula fluminea.* The dissimilarities may be due to: (a) taxonomic differences, (b) ecological differences, and/or, (c) experimental artifacts. *C. fluminea* belongs to another genus and *P. caroliniana* and *P. solida*, although congeneric, are placed in remotely related subgenera (*i.e. Polymesoda* and *Neocyrena;* Severeyn, 1993). The three species live in distinct habitats. *C. fluminea* inhabits freshwater, while both *Polymesoda* species are estuarine. *P. caroliniana* lives mostly in temperate conditions, while *P. solida* is exclusively tropical (Severeyn, 1993).

CONCLUSIONS

The populations of *Polymesoda solida* studied from Lake Maracaibo in western Venezuela developed from fertilized eggs to late-stage veligers (umbo) in five to seven days, but may prolong this up to one month. Observations also indicated that development is highly variable. After fertilization, the gastrula stage was reached in three h and the first larval stage, an encapsulated trochophore, in 12 hr. Under normal conditions, the capsule surrounding the trochophore disappeared 30 hr after fertilization and the straight-hinged veliger stage was reached in 48 hr. The advanced veliger or umbo stage appeared two days later. Sometimes, the capsule persisted and the trochophore was able to continue its development within it. Larvae that remained encapsulated reached the straight-hinged veliger stage and can persist as such up to one month. After this, the larvae died. The prolonged encapsulated phase suggests that between the trochophore and the straight-hinged veliger stages, the larvae are able to use stored food reserves, probably originating in the egg reserves. It is also possible that some nutrients can diffuse through the capsule to be absorbed by the larva. Eventually the larva dies, if not liberated from the capsule.

Additional research must be done to answer a series of questions arising from this investigation. Are developmental times in nature similar to those reported here? Are the prolonged encapsulated stages present in nature? What conditions stimulate the maintenance of the capsule or allow it to dissolve? Does the capsule allow diffusion of nutrients into it? If not, how can the larvae survive such a long period (up to a month) without an external food supply? Does the capsule increase bouyancy and the likelihood of long-term dispersal? How can salinity changes affect larval stages within the capsule? Why was it not possible to achieve metamorphosis of *Polymesoda solida* under our laboratory conditions?

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Gametogenic cycle of the Carolina marshclam, *Polymesoda caroliniana* (Bosc, 1801), from coastal Georgia

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Abstract. The gametogenic cycle of a brackish water bivalve, *Polymesoda caroliniana* (Bosc, 1801), was studied from December 1983 to February 1986 on Skidaway Island, Georgia, U.S.A. The population studied occurred in an irregularly flooded mosquito-control ditch which drains into the Skidaway River. Staging criteria were used to describe gametogenic development from histological preparations. Several features were quantitatively analyzed for males (% gonad area and % spermatozoa area) and females (% gonad area, % oocyte area, and egg number) using photo-planimetry (image analysis). A unimodal gametogenic cycle was evident in 1984 and 1985. In 1984, late development occurred from December 1983 to July 1984 with ripe individuals occurring from June to September. Spawning occurred in August and September. In 1985, ripe individuals occurred in July and August with spawning occurring in August and September. Gonadal area levels were consistent from year to year. Males and females produced similar amounts of gametes during 1985, while males had significantly higher levels and a more protracted spawning period during 1984. Sex ratios were 1:1 with no hermaphrodites detected.

Although the Carolina marshclam, *Polymesoda caroliniana* (Bosc, 1801) (Bivalvia: Corbiculidae), is a dominant macro-invertebrate within the brackish water of southeastern U.S. and Gulf of Mexico marshes, little is known of its biology. *P. caroliniana* ranges from Virginia to Mexico (Schalie, 1933) and occurs intertidally among the root mats of various marsh plant species (Harry, 1942; Andrews and Cook, 1951) or on muddy creek banks and bottoms (Schalie, 1933; Tabb and Moore, 1971; Hoese, 1973). Schalie (1933) described the distribution, shell morphology, and anatomy of *P. caroliniana,* while Olsen (1972, 1975) characterized it as a non-selective filter feeder. Fairbanks (1963) observed that the spawning period of *P. caroliniana* overlaps with that of another brackish water bivalve, *Rangia cuneata* (Sowerby, 1831), in Louisiana, while Duobinis and Hackney (1978) briefly described *P. caroliniana* recruitment periods (February and July) in Mississippi.

Polymesoda caroliniana spawns from July to September in a population on the northwest Florida Gulf coast (Olsen, 1976). In an irregularly flooded population in the Mississippi marsh, ripe *P. caroliniana* individuals were found in May, July, August, and October (Hackney, 1983). Hackney (1983) was uncertain whether this indicated a prolonged single breeding period or three discrete spawning periods. No studies on the gametogenic cycle of *P. caroliniana* from Atlantic coastal populations have been undertaken. Due to the dearth of life history information on this species, its importance as a macroconsumer, and its abundance within the salt-marsh ecosystem, the reproductive cycle of *P. caroliniana* for a population from the estuarine waters of Georgia is described.

MATERIALS AND METHODS

Sampling and Tissue Processing

A mean of 19.6 (range 15-20) *Polymesoda caroliniana* individuals was collected monthly from December 1983 to February 1986 from a mosquito-control ditch located on the northwestern tip of Skidaway Island, Georgia. These ditches occur within a maritime forest and drain into the Skidaway River. The ditch-water salinity ranged from 0 ppt during rain runoff at low tide to 28 ppt on high spring tides. Clams occurred at the elevated end of the ditch and were irregularly covered by the tides. They were obtained from a mud substrate within the root mat of salt marsh grasses, *Spartina alternata* Loisel and *Juncus roamerianus* Scheele. Shell length measurements and tissue processing (histology) were performed as described previously (Heffernan *et al.*, 1989a, b). Individuals ranged in shell length (longest possible measurement, *i.e.* anterior-posterior) from 14.6 to 33.6 mm, with a mean of 25.9 mm.

Qualitative Reproductive Analysis

The staging criteria described by Morton (1985) were employed for comparative purposes. Individuals were thus ascribed, on the basis of morphological observations, to one of the following stages: Inactive; Male or Female Developing; Male or Female Ripe; Male or Female Partially Spawned; and Male or Female Spent. Monthly gonad index (GI) values were computed (as described previously, Heffernan *et al.*, 1989a, b) using the following developmental stage scoring system: Inactive = 1; Developing = 4; Ripe = 5; Partially Spawned = 3; and Spent = 2.

Quantitative Reproductive Analysis

Two fields per specimen with a minimum separation of 80-100 µm (more often ca. 300 µm) within the tissue block were printed on a Javelin[1] video printer via a TV camera system mounted on a standard compound microscope (10x objective) (Heffernan and Walker, 1989a). These prints contained elements of epithelial, gonadal, connective, and digestive tissues and had a standard field size of 7,566 mm^2. Given a mean magnification factor of 244.9 x (± 2.1, SE) this represents an actual field area of 0.125 mm^2.[2]

Using total field area as the standard, several male and female area measurements were calculated from prints using a Sigma-Scan[1] digitizing tablet, and expressed as percentage values. We have termed this method of image analysis "photo-planimetry." Thus, mean values calculated from data measured on both specimen prints were evaluated for each individual, depending on sex, for the following: Males - % Gonad and % Spermatozoa; Females - % Gonad, % Eggs, and Egg Number (manually counted). The percentage values indicate how much of the field area was occupied by the gametogenic feature being measured, *e.g.* egg area. Sex ratios were tested against a 1:1 ratio with Chi-square tests (Steel and Torrie, 1960).

RESULTS

The gametogenic cycle of *Polymesoda caroliniana* from Skidaway Island, was ascertained from the combination of qualitative and quantitative data collected from December 1983 to February 1986. Monthly qualitative and quantitative data assessments of reproductive conditions are illustrated in Figs. 1 and 2 and Figs. 3 and 4, respectively. In Georgia, *P. caroliniana* displayed an unimodal gametogenic cycle, with spawning in the late summer in both years studied.

1984-1985 SPERMATOGENESIS

In 1984, late developmental stages of maturation were present from December 1983 to July 1984 with the percentage of ripe stages dominant in July and August (Fig. 1). Partial spawning commenced in August with the majority of animals having spawned by September. Presumably (no data gathered in October), spawning continued through December, although at a reduced level. During November and December early maturation stages dominated. Mean monthly gonad index values for males and females were tested by analysis of variance. Overall, no significant differences between males and females were detected (P = 0.3382) (Fig. 2). In 1985, early stages of maturation dominated until March (25%) and July (20%) when late and ripe stages (20%) occurred (Fig. 1). Mean gonad index did not change significantly for males from December 1983 to June 1984 before a significant increase to 4.2 occurred in July. The male gonad index decreased significantly in August and September, indicating spawning. By August, late stages dominated with some spawning occurring. Spawning animals dominated in September. Early maturation stages were present for the remainder of the year. Analysis of gonad indices (GI) (Fig. 2) revealed no significant change in GI from January to April, but a significant drop from April to May (2.9 to 2.3). This drop in GI values was followed by a rapid and significant increase from May to August (3.6). A significantly rapid drop in values from 3.6 to 2.6 occurred from August to September, indicating spawning. A significant increase in value occurred from September (2.6) to October (3.4), with no significant change in values thereafter until March 1986. The drop in GI in April-May is indicative of spawning, but neither the staging data (Fig. 1) nor the quantitative data support this suggestion. The decline in August-September does reflect spawning and quantitative data support this.

The quantitative data for males revealed that percent total field area of gonadal tissue remained at approximately 57%, with no significant changes from December 1983 to June 1984 (Fig. 3A). No significant differences in percent total field area for gonadal tissue (ca. 62%) occurred from November 1984 to February 1986, with the exception of the significant drop in May 1985. Although no significant differences in percent lumen (*i.e.* field area occupied by follicle lumena) in males were detected between the months from February 1984 to September 1984, an obvious decline was present from May to July. The large standard error present in the June sample resulted

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[1] Mention of a trade name does not signify endorsement by the University of Georgia.

[2] Enforced camera (TV) replacement during the course of the study required replacement of prints taken with the original system. Consequently, the presently reported field dimensions differ unavoidably, due to the differing magnification factors of the two TV cameras, from those reported in an earlier Research Note (Heffernan and Walker, 1989a). Those dimensions were based solely on data generated by the original camera system.

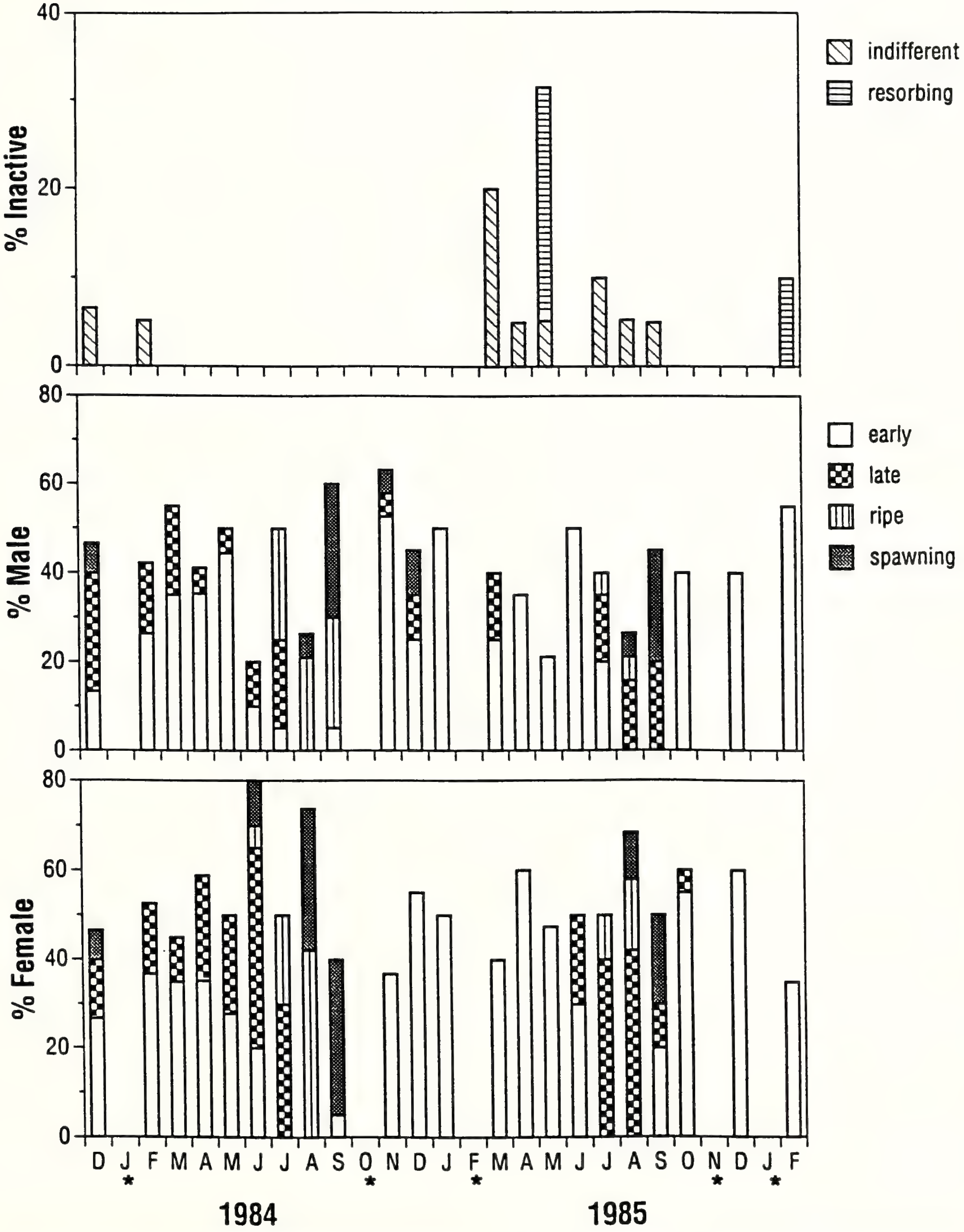

Fig. 1. Qualitative data illustrating the sex and gonad developmental stages of *Polymesoda caroliniana* from a Skidaway Island, Georgia population. The length of each area represents the percentage frequency of clams in each developmental stage. (*, no sampling).

in no significant difference being determined in the data between May and July for pair-wise comparisons; however, it was obvious that significant differences occurred between the May (7%) and July (ca. 0%) data. The lumen percentage remained at approximately 0% until October before increasing to 5% in November. The lumen percentage remained at approximately 4% until March 1985 before increasing to 7% in April. In month-wise comparisons, no significant increase was revealed due to large standard errors in the May sample; however, April and May values were significantly higher than the July and August values. After August, values increased and remained at approximately 5% during the remainder of the study.

The area occupied by sperm tissue remained at approximately 8% to 9% (of field) from December 1983 to July 1984 before significantly increasing and peaking in August and September 1984. The sperm percentage significantly dropped to approximately 4% by November and remained at this level until April. Thus, males matured in both years by August and spawned by October in 1985 and by at least November in 1984 (October 1984 data absent). These quantitative data support the conclusion that a unimodal male gametogenic cycle occurs in this Georgia population of *P. caroliniana.*

1984-1985 OOGENESIS

In 1984, early maturation stages were dominant in animals from December 1983 to May 1984, although late maturation stages were present (Fig. 1). In June, late maturation stages were dominant with some animals ripe and spawning. By July, all animals were in the late maturation or ripe stage. Ripe individuals (41%) were dominant in August with 36% being in the spawning stage. Spawning individuals were dominant (36%) in September. Individuals were in the early maturation stages from November to May 1985. In June 1985, late maturation stages were observed and became the dominant stage until August. Ripe stages were present in July and August, with spawning occurring in August and September. Animals in the early stage of maturation were present throughout the remainder of the study. As was the case in males, female GI data supported the staging data. Female GI remained constant from December 1983 to June 1984 before significantly increasing to a maximum (4.2) in July. Significant declines occurred from July to September. GI levels reached a plateau again from November 1984 until May 1985 before a rapid increase occurred. Female GI levels peaked in July (4.1) before significantly dropping in August and September. GI levels reached a plateau again by October 1985.

Quantitative data for the female showed that gonadal tissue remained consistent, at approximately 55% (of field), from January until June 1984. In 1985 this value was slightly higher (60%) from November 1984 to June 1985. Rapid reductions in gonadal tissue area occurred between June, July, and August 1984 (Fig. 4A). No significant differences occurred between August and September 1984. In 1985, similar significant reductions occurred between June and July with no significant differences being detected between July and September. These reductions in percent total field area occupied by gonadal tissue occurred during the period corresponding to late development and

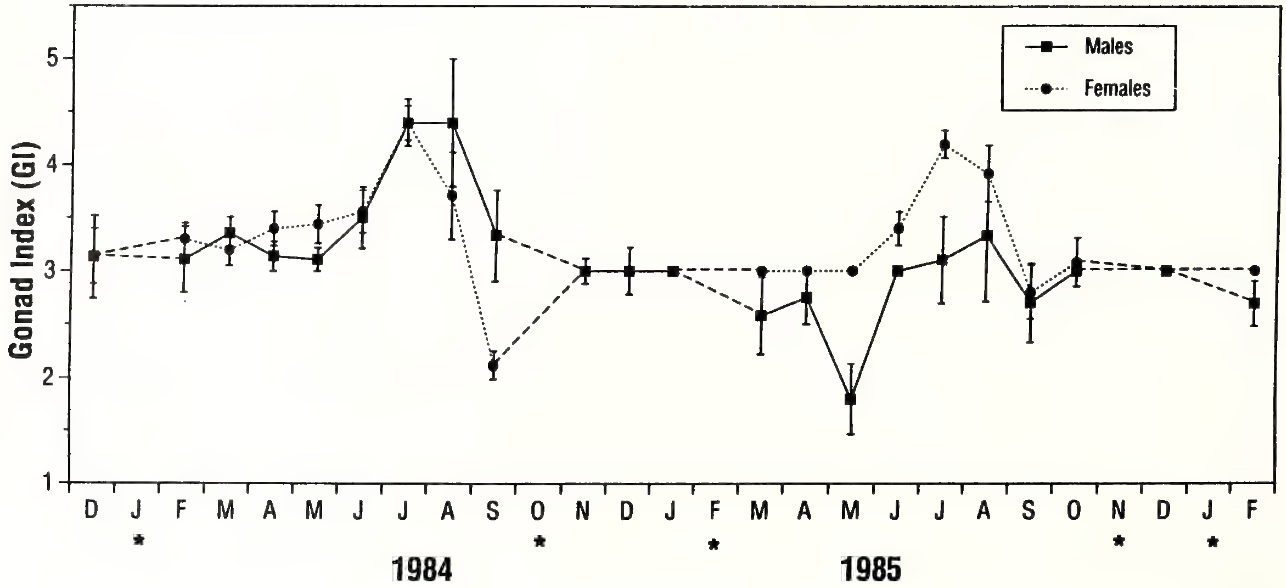

Fig. 2. Gonad index values for male and female *Polymesoda caroliniana* in a population from Skidaway Island, Georgia. (*, no sampling).

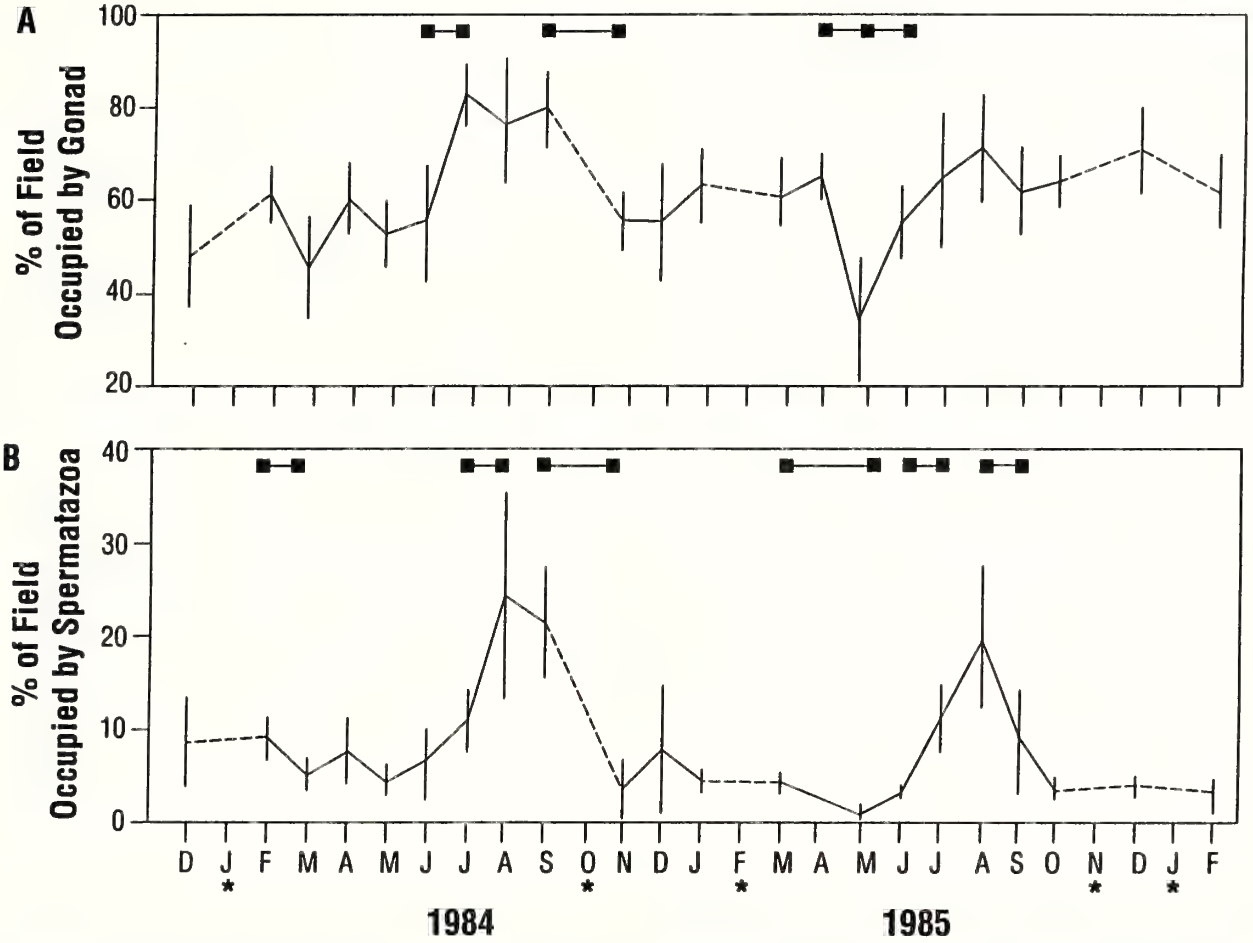

Fig. 3. Composite of quantitative data (obtained using image analysis of print microscopic fields) representing the state of gonad conditions for *Polymesoda caroliniana* males from Skidaway Island, Georgia population. (A) Mean percentage of print field area occupied by gonad. (B) Mean percentage of print field area occupied by spermatozoa. Vertical bars represent two standard errors above the mean. Horizontal bars indicate periods of statistically significant (t-tests) changes in the features being measured. These have been included to highlight likely spawning events. (*, no sampling).

maturity (ripe stages). Minimum values were obtained during spawning periods (August-September 1984 and July-August 1985). Area occupied by oocytes (Fig. 4B), displayed no significant changes from February 1984 to June 1984 and from November 1984 to June 1985. Significant decreases in gonadal area occupied by oocytes occurred from June to September in both years. Mean number of eggs (Fig. 4C) remained at zero from December 1983 to May 1984 and from November 1984 to June 1985. Egg production (mean number of eggs) peaked in July of both years (Table 1). In 1984, egg production remained high through September (*i.e.* no significant differences) and dropped to zero by November. In 1985, a significant reduction in egg production occurred in August and reached zero production by September. The two sets of quantitative data thus reveal a unimodal spawning peak from August to September confirming qualitative results.

Table 1. Gametogenic peak production values for *Polymesoda caroliniana* during 1984 and 1985. Data given in % area or number of eggs ± one standard error. (NS, not significant; Sign., significance).

	1984	1985	t-test	df	Sign.
Female					
% Gonad	55.9 ± 2.9 (June)	57.3 ± 5.2 (June)	0.230	16	NS
% Egg	14.3 ± 1.5 (Aug)	18.7 ± 2.0 (July)	1.730	19	NS
# Egg	30.4 ± 2.7 (July)	34.3 ± 4.1 (July)	0.792	17	NS
Male					
% Gonad	83.4 ± 3.3 (July)	71.6 ± 5.9 (Aug)	1.760	8	NS
% Sperm	24.3 ± 5.5 (Aug)	19.9 ± 3.8 (Aug)	0.663	10	NS

COMPARISON OF YEARLY DATA

Comparison of spawning events for *Polymesoda caroliniana* between years reveal similar patterns (major spawning in August and September) in both years. Yet, during 1984, a protracted spawning period occurred for both males and females, as compared to 1985, as indicated by the qualitative (Fig. 1) and quantitative data (Figs. 3, 4). In 1984, spawning in the males and females appeared to be extended, as evidenced by females spawning in June, August and September and males spawning in August, September, October and November (Fig. 1) and by the plateauing effect observed in the quantitative data for 1984 (Figs. 3, 4). For the percentage of sperm tissue, a peak was obtained in August 1984 with no significant differences detected between August and September (thus a plateau) before the significant drop by November (Fig. 3C). Mean egg count peaked in July and did not decrease significantly until September, before dropping to zero by November. In 1985, values rapidly increased from June to a July peak and then significantly dropped by August. Thus, no plateauing effect occurred and a more rapid spawning event resulted in 1985, as compared to 1984.

Although a more protracted spawning event occurred in 1984 as compared to 1985, gametogenic production levels each year were equal (Table 1). There were no significant differences in male gonadal area or spermatozoa levels at maturity during 1984 and 1985. Similarly, female gonadal area, oocyte area and mean number of eggs were equal each year (Table 2).

Polymesoda caroliniana is dioecious. Individuals ($N = 425$) ranging from 14.6 to 33.6 mm in shell length were sexed during this study. Females ($N = 224$) slightly outnumbered males ($N = 201$), but the ratio did not significantly differ (Chi-square = 1.24, $p > 0.05$) from an equal (1:1) sex ratio. No hermaphrodites were detected.

Mean ambient sea water temperature and salinity data for the Skidaway River are given in Fig. 5. Ambient sea water temperatures peaked in August 1984 and early September 1985.

DISCUSSION

The *Polymesoda caroliniana* population from a high marsh site in Georgia has a single spawning season occurring in August and September. The unimodal gametogenic cycle of *P. caroliniana* described herein for a coastal Georgia population is similar to the patterns described for populations in the northwest Florida Gulf coast and a Mississippi marsh. Olsen (1976) observed a unimodal spawning pattern from July to September in a Florida population, which is similar to our observed pattern of August-September spawning during 1985 (Fig. 1). Hackney (1983) observed ripe *P. caroliniana* individuals in Mississippi in May, July, August and October, but was uncertain whether this indicated a single prolonged breeding period or three distinct spawning periods. The spawning pattern exhibited in Mississippi is similar to the Georgia *P. caroliniana* spawning pattern of 1984, where spawning was observed in June and again in August-September for females and from August-September and then November-December for males (Fig. 1). Unfortunately, an October sample was not taken in 1984, so we do not know if the male pattern is

Table 2. Comparison of gonadal production levels among ripe males and females of *Polymesoda caroliniana* at the Skidaway Island site during 1984 and 1985 and three other bivalve species from populations at House Creek, Little Tybee Island, Georgia. (NS, not significant; S, significant; Sign., significance).

	Gonadal Area (%)			Gamete Area (%)		
	Male	Female	Sign.	Sperm	Ova	Sign.
A. *Polymesoda caroliniana*						
1984	83.4	55.9 (June)	S ($p < 0.001$)	24.3	14.3 (Aug.)	NS
1985	57.5	71.6 (Aug./May)	NS	19.9	18.7 (Aug./July)	NS
B. *Geukensia demissa* (from Heffernan and Walker, 1989b)						
1984	54.1 (5.2)-Jul.	40.2 (5.3)-Jul.	NS	24.0 (2.3)-Aug.	33.3 (2.2)-Aug.	S ($p < 0.02$)
1985	59.7 (2.4)-Jul.	54.9 (6.6)-Jul.	NS	27.0 (1.4)-Jul.	29.5 (3.9)-Jul.	NS
C. *Mercenaria mercenaria* (from Heffernan *et al.*, 1989a)						
1984 Spring	94.5 (1.4)-Feb.	94.3 (1.4)-Mar.	NS	38.9 (4.5)-Mar.	33.6 (2.2)-Mar.	NS
1984 Fall	91.4 (2.1)-Sept.	92.5 (1.8)-Sept.	NS	32.1 (1.6)-Aug.	21.5 (1.0)-Sept.	S ($p < 0.001$)
1985 Spring	90.0 (2.2)-Jan.	96.5 (1.1)-Jan.	NS	67.1 (4.4)-Apr.	26.5 (0.7)-Mar.	S ($p < 0.001$)
1985 Fall	92.7 (1.0)-Sept.	95.3 (1.6)-Sept.	NS	16.0 (1.5)-Sept.	19.0 (1.9)-Sept.	NS
1985 Winter	93.4 (1.1)-Dec.	92.0 (1.9)-Nov.	NS	28.4 (3.0)-Dec.	23.9 (0.6)-Dec.	NS
D. *Crassostrea virginica* (from Heffernan *et al.*, 1989b)						
1984	85.1 (7.4)-Apr.	64.4 (9.8)-Jul.	NS	28.3 (2.3)-Apr.	22.3 (4.2)-Jul.	NS
	96.9 (0.7)-Jun.	99.6 (0.8)-Jun.	NS	52.7 (4.2)-Jun.	44.3 (4.1)-Jun.	NS

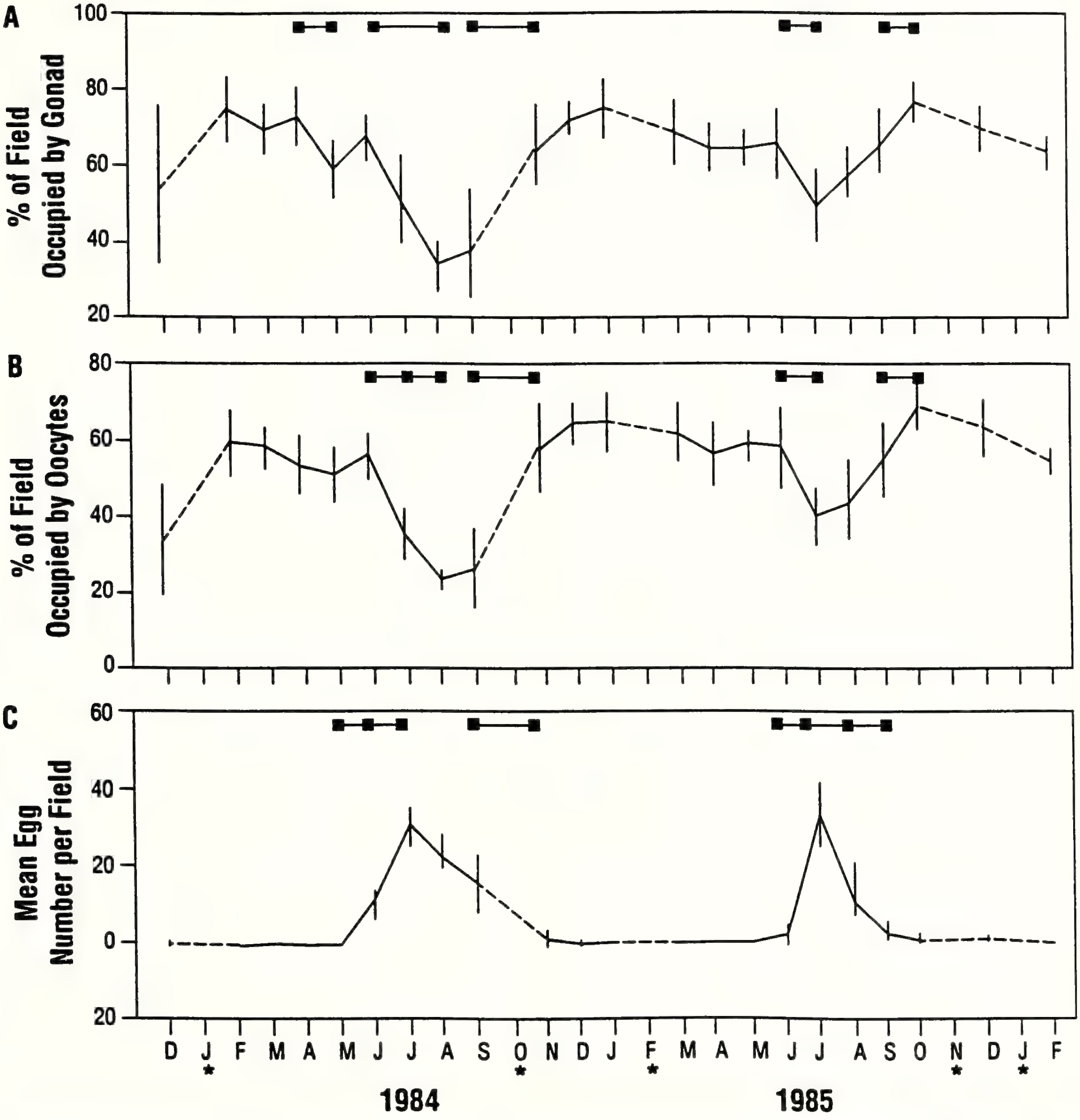

Fig. 4. Composite of quantitative data (obtained using image analysis of print fields) representing the state of gonadal condition for *Polymesoda caroliniana* females from Skidaway Island, Georgia population. (A) Mean percentage of print field area occupied by gonad. (B) Mean percentage of print field area occupied by oocytes. (C) Mean number of eggs per print field area. Vertical bars represent two standard errors above the mean. Horizontal bars indicate periods of statistically significant (t-tests) changes in the features being measured. These have been included to highlight likely spawning events. (*, no sampling).

truly unimodal or bimodal. Hackney (1983) observed no ripe individuals in either his June or September samples, *i.e.* periods between spawnings, leading him to consider that three spawning periods occurred. In our data, the percentage of ripe individuals increased from June to August, with ripe individuals occurring in July, leading us to believe that in Georgia one spawning event occurs. The quantitative data also supports a unimodal spawning event for *P. caroliniana* in this Georgia population.

Our results are also similar to the spawning pattern observed for *Polymesoda erosa* (Solander, 1786) from a Hong Kong mangrove population. *P. erosa* commences

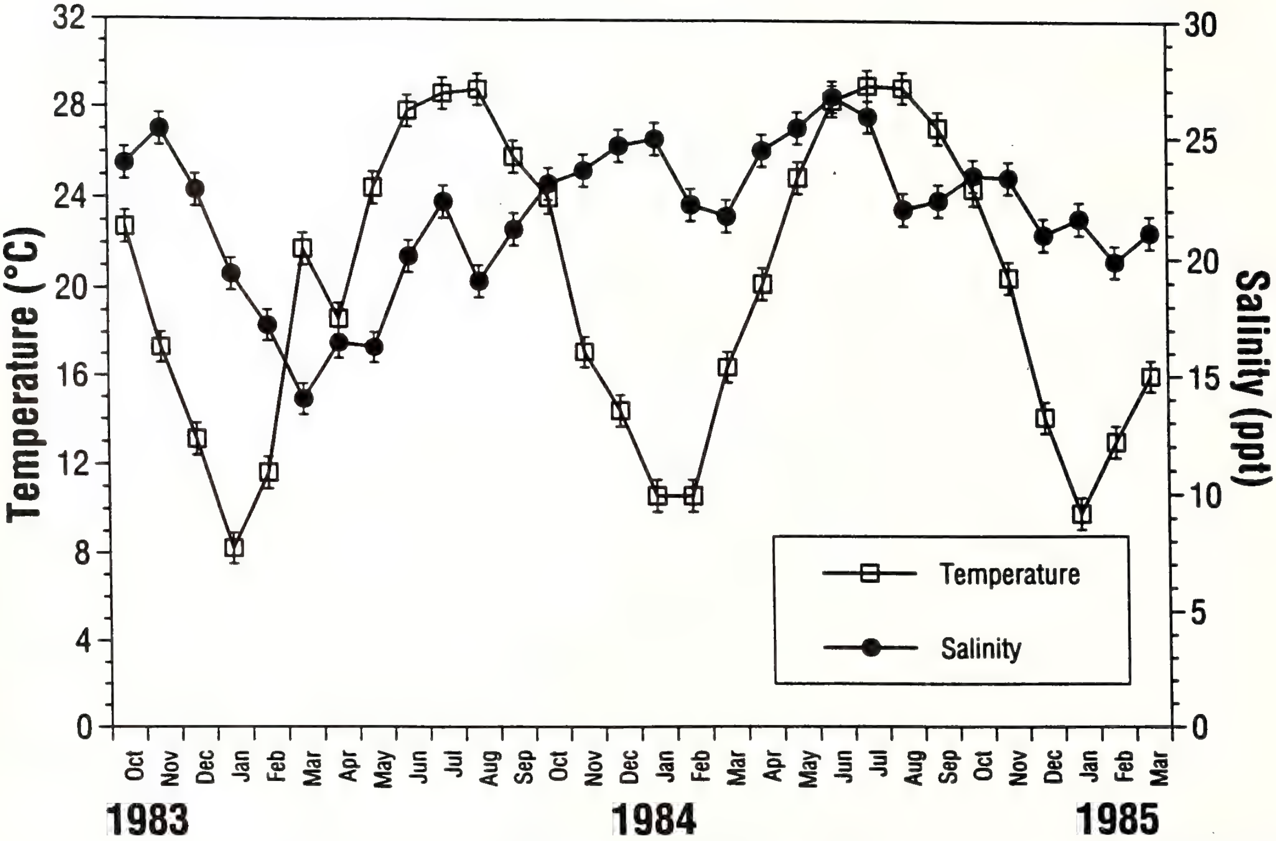

Fig. 5. Mean ambient water temperatures and salinities for the Skidaway River that occasionally inundates the *Polymesoda caroliniana* population located in an irregularly flooded mosquito-control ditch on Skidaway Island, Georgia.

active gametogenesis in April and May and by June mature gametes occur with spawning taking place during summer (Morton, 1985). This type of reproductive pattern is similar to our 1985 results, where late active stages were first observed in June and spawning finished by September. However, it differs from the 1984 results where late active stages were present from December 1983 through July 1984. In 1984 females spawned from June to possibly October, while males spawned from August until December. Obviously, temporal effects between years can alter the gametogenic cycle of a species.

Temporal differences in gametogenic cycles have been recorded for other Georgia bivalves. Three bivalve species collected from the same site in Wassaw Sound showed marked differences in their reproductive patterns between 1984 and 1985. *Mercenaria mercenaria* (Linné, 1758) showed evidence of trimodal spawning in 1984, but bimodal spawning in 1985 (Heffernan *et al.*, 1989a). *Crassostrea virginica* (Gmelin, 1791) showed evidence of spawning from June to November in 1984, but only from August to November in 1985 (Heffernan *et al.*, 1989b). *Geukensia demissa* (Dillwyn, 1817) spawned from August to either October (females) or December (males) in 1984, but only from July to September in 1985 (both sexes) (Heffernan and Walker, 1989b). In a *Spisula solidissima similis* (Say, 1822) population in coastal Georgia, clams spawned from March to May in 1990, but from April to June in 1991 (Kanti *et al.*, 1993).

Equal gametogenic production levels between years, even with different timing patterns (protracted or rapid), have been recorded in other studies (Table 2). Gonadal area levels of *Geukensia demissa* were consistent from year to year (Heffernan and Walker, 1989b). *G. demissa* males and females produced similar amounts of gametes in 1985, but females had a significantly higher output of gametes in 1984. In *Mercenaria mercenaria* and *Crassostrea virginica* (*fide* Heffernan *et al.*, 1989a, b), greater levels of reproductive output were detected in 1985 than in 1984. Thus, temporal variations may or may not occur within populations. In the two cases where temporal variations did not occur (*Geukensia* and *Polymesoda*), there is a relatively short spawning season. When temporal variations were detected, either a polymodal *(Mercenaria)* or a prolonged spawning season occurs *(Crassostrea)* from May to October.

For *Polymesoda caroliniana*, clams in 1984 had a much more protracted spawning period than in 1985, although gametogenic production levels each year were equal (Table 1). The factor(s) responsible for the observed temporal variations in gametogenesis between years is unknown. Temperature is a major factor in controlling gametogenesis in marine bivalves (Giese, 1959). For *Spisula solidissima* (Dillwyn, 1817) populations, Ropes (1968) noted that clams generally spawned once per year when lower water temperatures prevailed, whereas, in warm-water years, clams spawned twice. For *Mercenaria mercenaria* in Georgia, Heffernan *et al.* (1989a) observed that clams spawned for a third time during a warmer than usual winter, whereas, clams previously spawned only in spring and fall. For *P. caroliniana* in this study, water temperature patterns for 1984 and 1985 were similar (Fig. 5).

Salinity can also regulate gametogenesis in marine bivalves (Giese, 1959). For *Polymesoda caroliniana* in this study, differences in salinity were observed between years, with salinities dropping lower during winter 1984 than in winter 1985. Although differences in salinity patterns were observed between years in this study (Fig. 5), salinity readings from the Skidaway River, into which these drainage ditches empty, are not necessarily reflective of salinities within the ditches at any one point in time. These ditches are flooded irregularly by the tide. During low tide, rain runoff can drastically alter the salinity within the ditches, as compared to the relatively vast volume of water in the river. These periodic changes in salinity due to rain runoff can play a role in regulating the gametogenic cycle of *P. caroliniana,* but the dynamics of the interaction between changes in salinity and spawning of *P. caroliniana* are unknown.

An examination of gametogenic production levels (% gonad area) from each sex during peak maturity periods, reveal that males had higher production levels than females in 1984, while production levels were equal in 1985 (Table 2A). In similar studies, no significant differences in gonadal area between sexes were recorded for *Geukensia demissa* (Table 2B), *Mercenaria mercenaria* (Table 2C), and *Crassostrea virginica* (Table 2D); however, significant differences in percent gamete area between sexes per year were detected in one year for *G. demissa* (Table 2B) and during the spring spawning of 1985 for *M. mercenaria* (Table 2C). In other reproductive studies, females of the Iceland scallop, *Chlamys islandica* (Müller, 1776) showed higher ova production values than males for sperm production (Sundet and Lee, 1984; Vahl and Sundet, 1985). Obviously, much variation within reproductive physiology can occur between years as well as between sexes within a year. The dynamics controlling such events are not well defined.

Based on the results of this study, *Polymesoda caroliniana* is dioecious. Sex ratio did not deviate significantly from 1:1 during this study and no hermaphrodites were recorded. Unfortunately, neither Olsen (1976) nor Hackney (1983) gave information pertaining to sex ratio in their studies; however, Olsen (1976) did note that no hermaphrodites were recorded among the 236 individuals examined. *Polymesoda erosa* is also dioecious and of the 167 specimens examined in Hong Kong, 51.5% were females, 38.5% males, 0.5% hermaphrodites and 9.5% indeterminate sex (Morton, 1985).

The results of this study should be interpreted with care when expanding the data to reproduction of the *P. caroliniana* population of coastal Georgia. *P. caroliniana* occurs in a variety of habitats within the coastal waters of Georgia. In higher saline areas, *P. caroliniana* occurs high in the intertidal zone usually either in small creeks or salt marsh areas that receive rain runoff; whereas, in brackish water areas farther inshore, clams can occur lower in the intertidal zone and onto subtidal creek bottoms (Walker, pers. obs.). The reproductive cycle of clams from more brackish and less hostile (in terms of length of aerial exposure time) environments can be different in timing and length of spawning.

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Morphometric and biochemical changes in two age classes of the tropical scallop, *Argopecten ventricosus,* under laboratory conditions

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Abstract. A laboratory study was carried out in Lewes, Delaware, U.S.A., to (a) compare, through controlled laboratory experiments, morphometric and biochemical changes in the digestive gland, adductor muscle, mantle-gills and gonad of eight- and 16-month-old tropical scallops *Argopecten ventricosus* (Sowerby, 1842), and (b) determine the effect of age on the content of carbohydrates and protein in the gonad.

The gonadal index of eight- and 16-month-old scallops declined through the first 40 days of the experiment. Also, carbohydrate content declined significantly in the digestive gland and adductor muscle. This suggests energy was used either for somatic growth and/or reproduction. Some carbohydrates could have been used for reproduction, but were not transferred directly to the gonad before day 40.

Adductor muscle dry weight and protein content of eight- and 16-month-old scallops increased for the first 40 days of the experiment, then declined around day 55. Simultaneously, around day 55, both groups of scallops had noticeable increases in gonadal dry weight and protein content. This suggests that the adductor muscle stores protein during the first 40 days, then protein catabolism in the adductor muscle contributes to reproductive activity of the gonad.

Protein content in the mantle was higher in eight- than in 16-month-old scallops. This suggests mantle-gill protein provides better support for somatic growth in eight- than in 16-month old tropical scallops. The laboratory study in Delaware suggests that one-year-old scallops will spawn in the field in March.

The reproductive cycle of bivalves includes the following stages: (a) vegetative (juveniles); (b) activation; (c) growth and gametogenesis; (d) maturation; (e) resting stage. According to Sastry (1975) the timing of the reproductive cycle is a genetic response to the environment, and involves interaction of exogenous and endogenous factors. Giese (1959) identified the exogenous factors as temperature, salinity, day length and food abundance; endogenous factors included age, metabolism and neuroendocrines.

Age is an endogenous factor affecting gametogenesis in scallops (Barber and Blake, 1991). With a reduction in the rate of somatic growth as scallops increase in size, increase in the energy allocated for gamete production occurs. According to Bayne and Newell (1983) this process of redistribution from somatic to reproductive energy sets the limit for species size. Thompson and MacDonald (1991) suggested there is a reduction in energy available for growth as the organism increases in size, depending on the combination of food available and efficiency to convert this food into tissue. However, according to Blake (1972) a minimum age (or size) is required for gametogenesis to begin in *Argopecten irradians* (Lamarck, 1819).

Scallops of different ages have distinct metabolisms. Small individuals invest more energy in growth than in reproduction. Bayne and Newell (1983) found a higher metabolic rate in smaller than in larger individuals of *Mytilus edulis* Linné, 1758.

Reproductive strategies used by scallops at different ages have been studied by several authors: *Argopecten irradians* by Bricelj *et al.* (1987) using physiological conditions, and Epp *et al.* (1988) using condition indices. Blake (1972) studied the interactions among age, temperature, neurosections and reproductive stage in *A. irradians*. Allocation of chemical compounds in different size classes of *Chlamys islandica* (Müller, 1776) was studied by Sundet and Vahl (1981) and in *A. purpuratus* (Lamarck, 1819) by Martinez (1991).

The literature indicates that bivalves can obtain energy either directly from food, or from storage substrates in organs and tissues, such as the digestive gland (Taylor and Venn, 1979), the adductor muscle (Ansell, 1974; Epp *et al.*, 1988), or the mantle (Barber and Blake, 1981; Lowe *et al.*, 1982). Also, a fluctuation in utilization of storage compounds (lipids, carbohydrates and proteins) has been observed in these bivalves relative to the reproductive cycle.

The objectives of this study were: (a) to compare, through controlled laboratory experiments, morphometric and biochemical changes in the digestive gland, adductor muscle, mantle-gills and gonad between eight- and 16-month-old tropical scallops, *Argopecten ventricosus* (Sowerby, 1842), and (b) to determine the effect of age on the content of carbohydrates and protein in the gonad of these scallops.

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MATERIALS AND METHODS

Two groups of *Argopecten ventricosus* were compared. One group (eight-month-old) was observed in November 1989, and a second (16-month-old) in May 1990.

REPRODUCTIVE CONDITION

Morphometric data were obtained from wet weights of the digestive gland, adductor muscle, mantle-gill and gonad. Indices for each organ were defined by the following formula:

$$\text{Index} = \frac{\text{dry weight of organ}}{\text{dry weight of soft parts}} \times 100$$

Biochemical determinations included carbohydrate and protein levels from the digestive gland, adductor muscle, mantle-gills and gonad. Determination of carbohydrates followed the technique presented by Barber and Blake (1981), using phenol in water and sulfuric acid, and reading the optical density at 490 nm (Lowry *et al.*, 1951; Mann and Gallager, 1985). Proteins were measured using the Bio-Rad Protein Assay (BIO RAD, Richmond, California), a dye-binding assay based on the differential color change of a dye in response to various concentrations of protein (Bradford, 1976).

CULTURE

Scallops were collected off Farallon Beach, Panama Bay, Panama, with a 1 m dredge, in 10 m depth. Animals were maintained in fiberglass tanks with running sea water in the marine laboratory of the University of Panama on Naos Island. Scallops (wrapped in wet towels, and held at 19°C) were transported by air to the College of Marine Studies in Lewes, Delaware, U.S.A., in September 1988.

In Lewes, 40 scallops were conditioned and maintained in a 200 l recirculating seawater tank at 19°C and 30 ppt salinity. A combined algal diet (50:50) of *Isochrysis galbana* Parke (C-ISO) and *Chaetoceros calcitrans* Paulsen was provided daily.

In February 1989, 20 scallops were induced to spawn by thermal stimulation (26°C) and frequent water changes. Larvae were reared in a 200 l tank at 24°C, and a combined algal diet was provided daily.

Eight-Month-Old Scallops

In October 1989, 90 eight-month-old scallops from the group spawned in February 1989 were separated into three groups (30 scallops each), and their sizes and weights were determined. Initial condition was analyzed for ten individuals by determining wet and dry weights of the digestive gland, adductor muscle, mantle-gills and gonad, and a biochemical analysis was performed for each organ.

Thirty of the 90 scallops were placed in each of three aquaria (40 l each) containing aerated filtered seawater. A combination of monocultures (50:50) of *Isochrysis galbana* (T-ISO) and *Chaetoceros gracilis* at high concentrations was added daily to the three aquaria (this phytoplankton concentration was observed in the field in Panama during the dry season). In addition, as a control, several scallops were placed in normal densities of phytoplankton observed during the dry season, and the amount of phytoplankton cleared by the scallops was determined. This experiment was performed every other week, to determine if sufficient food was being provided to the experimental scallops. Quantities of phytoplankton consumed by experimental scallops were determined daily by direct count with a hemocytometer and weekly with a Coulter Counter. The correction factor for a plateau in normal rate of growth of phytoplankton was determined by holding an aquarium with phytoplankton for only 24 h.

Three aquaria were maintained at 20°C, the temperature observed in the field in Panama during the dry season. Water temperature was maintained in a circulating bath (Forma Scientific). Salinity was measured daily using a refractometer; pH of the water was recorded daily.

In each of the three aquaria, ten scallops were sacrificed at 40 and again at 58 days. The condition of each scallop was determined by the wet and dry weights of the digestive diverticulum, adductor muscle, mantle-gills and gonad, and a biochemical analysis of each organ was performed. Morphometric measurements of scallops and mean levels of biochemical compounds were compared using ANOVA.

16-Month-Old Scallops

In May 1990, sizes and weights were determined for 150 *Argopecten ventricosus*, from the group spawned in the laboratory in February 1989. Initial condition was analyzed for ten individuals by determining dry weights of digestive gland, adductor muscle, mantle-gills and gonad. A biochemical analysis was also completed on ten scallops. At this time scallops ranged from 18 to 24 mm in size.

Sixty-nine of these scallops were placed in an aquarium containing filtered aerated seawater. These scallops were treated in a similar manner to those in the previous experiment.

Fifteen scallops from the experiment were sacrificed at 36 and again at 52 days. Wet and dry weights of the digestive gland, adductor muscle, mantle-gills and gonad of control and experimental scallops were determined. A biochemical analysis of these organs was also performed. Morphometric measurements of scallops and mean levels of biochemical compounds were statistically analyzed and compared with the group of eight-month-old scallops utilizing an ANOVA.

RESULTS

MORPHOMETRIC ANALYSIS

Eight- and 16-month-old scallops increased continuously and significantly in shell height during the experimental period (Fig. 1). Total weight increased significantly in both age classes to day 52, but declined in 16-month-old scallops after day 52 (Fig. 2).

Gonadal dry weight increased significantly in eight- and 16-month-old scallops during the experiment (Fig. 3). Gonadal index declined during the first 40 days of the experiment, then a significant increase occurred in both age classes (Fig. 4).

Digestive gland dry weight was stable in eight-month-old scallops until day 40 of the experiment, then declined by day 58 (Fig. 5). In 16-month-old scallops, digestive gland dry weight declined until day 36, then increased significantly by day 52 (Fig. 5).

Adductor muscle and mantle-gill dry weights of eight-month-old scallops increased until day 40 (Figs. 6 and 8). However, by day 58, weight of these organs either decreased or remained stable.

Adductor muscle and mantle-gill dry weights of 16-month-old scallops increased significantly during the experiment (Figs. 6 and 8). However, by day 58 the adductor muscle index had declined (Fig. 7).

BIOCHEMICAL ANALYSIS

Percent and content of glucose in the gonad were similar in the two age classes of scallops (Tables 1 and 2). Percent of gonadal protein was not statistically different (Table 3), although protein content was significantly higher in 16-month than in eight-month-old scallops (Table 4).

Glucose percent and content in the digestive gland and glucose percent in the mantle-gills were not significantly different between both age groups of scallops (Tables 1 and 2). Content of glucose in the mantle-gills was significantly higher in 16-month than in eight-month-old scallops.

Percent and content of protein in the digestive gland were not significantly different between both groups of scallops. However, percent and content of protein in the mantle-gills were significantly higher in eight-month than in 16-month-old scallops (Tables 3 and 4).

Percent and content of glucose in muscle were not significantly different between groups (Tables 1 and 2), but percent and content of protein in this organ were higher in eight-month than in 16-month-old scallops (Tables 3 and 4).

Table 1. Percent glucose of the digestive gland, adductor muscle, mantle-gill and gonad of *Argopecten ventricosus*.

Age	Day	Gland	Muscle	Mantle	Gonad
8	8	34.62	22.93	12.79	– –
8	40	8.84	2.99	4.32	4.60
8	58	12.22	– –	2.55	12.91
16	1	27.57	24.04	7.73	7.81
16	36	15.08	8.24	8.01	7.78
16	52	26.12	21.31	8.31	2.39

Table 2. Mean glucose content (standard error in parentheses) of the digestive gland, adductor muscle, mantle-gill and gonad of *Argopecten ventricosus*.

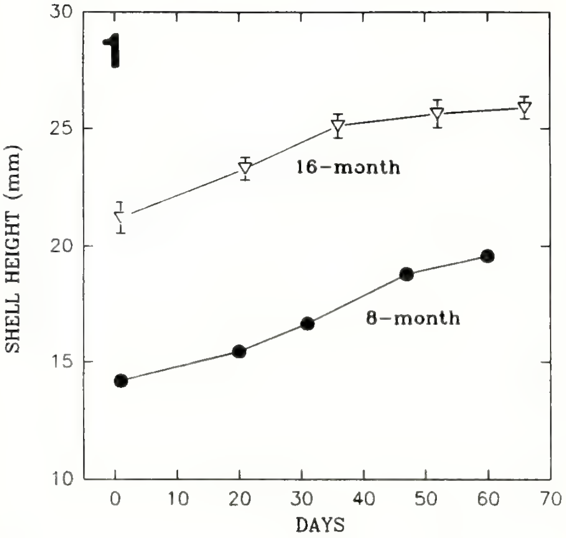
Age	Day	Gland	Muscle	Mantle	Gonad
8	8	5.44	4.16	1.38	– –
		(1.15)	(2.21)	(0.88)	
8	40	1.54	1.72	0.94	0.03
		(0.85)	(1.94)	(0.84)	
8	58	1.51	– –	0.34	0.04
		(0.30)		(0.12)	
16	1	5.76	10.33	1.75	0.24
		(2.32)	(2.77)	(0.59)	
16	36	2.36	3.42	1.57	0.48
		(2.57)	(3.40)	(1.75)	
16	52	8.04	14.64	3.62	0.16
		(5.72)	(8.77)	(2.66)	

Table 3. Percent protein of the digestive gland, adductor muscle, mantle-gills and gonad of *Argopecten ventricosus*.

Age	Day	Gland	Muscle	Mantle	Gonad
8	8	7.91	22.31	19.87	9.48
8	40	12.99	45.52	32.82	7.58
8	58	9.28	– –	9.69	15.38
16	1	10.87	15.87	11.49	14.76
16	36	9.78	24.50	8.97	7.58
16	52	14.91	22.34	12.41	7.04

Table 4. Mean protein content (standard error in parentheses) of the digestive gland, adductor muscle, mantle-gills and gonad of *Argopecten ventricosus*.

Age	Day	Gland	Muscle	Mantle	Gonad
8	8	1.36	4.22	2.87	0.05
		(1.11)	(2.30)	(1.80)	
8	40	2.11	20.42	7.72	0.13
		(0.82)	(15.06)	(7.45)	
8	58	1.35	– –	1.67	0.10
		(0.77)		(0.71)	
16	1	2.21	7.07	2.88	0.46
		(0.59)	(4.30)	(1.68)	
16	36	1.49	10.45	1.65	0.47
		(0.60)	(6.44)	(0.40)	
16	52	4.17	17.87	4.93	0.47
		(2.29)	(12.55)	(1.82)	


1
SHELL HEIGHT (mm)
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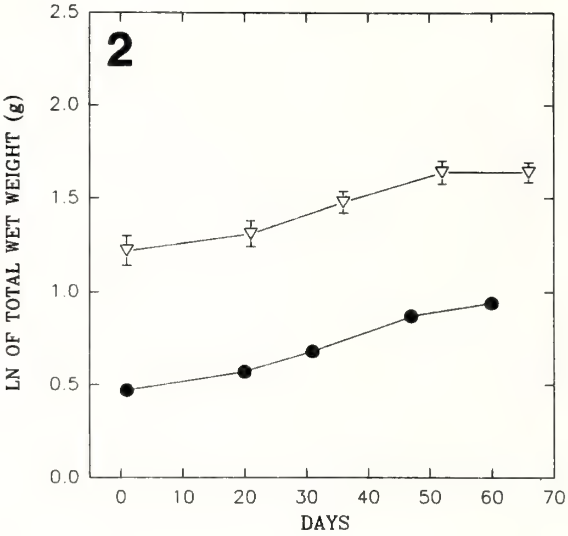
25
20
15
10
16-month
8-month
0
10
20
30
40
50
60
70
DAYS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LN OF TOTAL WET WEIGHT (g)
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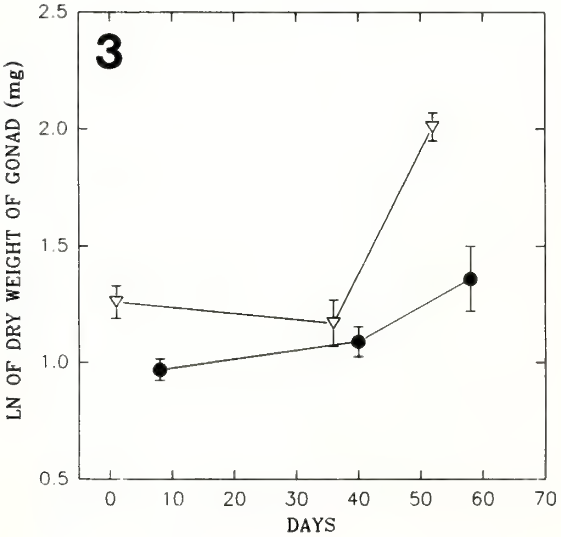
2.0
1.5
1.0
0.5
0.0
0
10
20
30
40
50
60
70
DAYS


3
LN OF DRY WEIGHT OF GONAD (mg)
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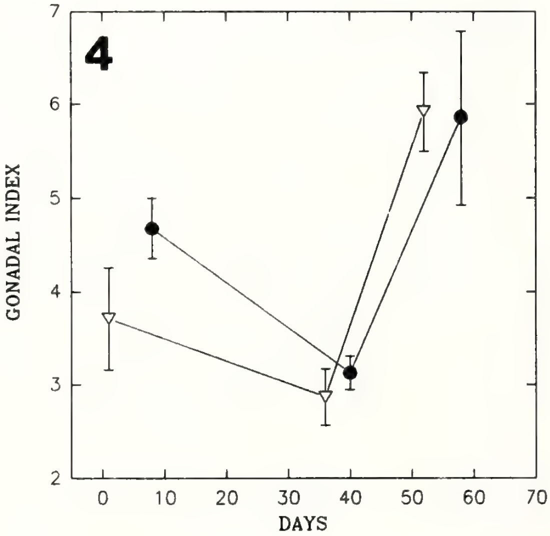
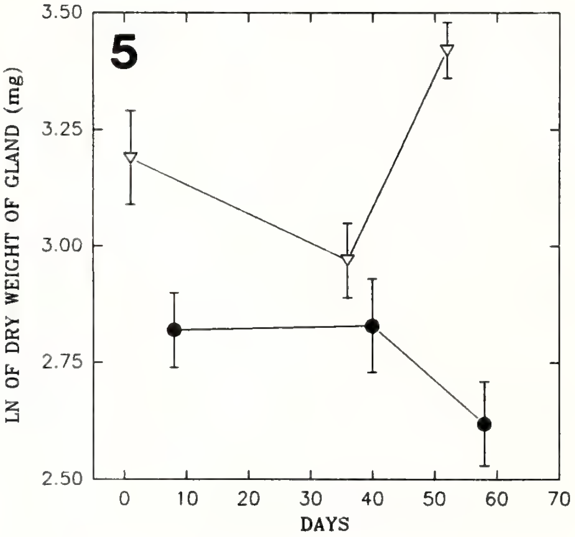
2.0
1.5
1.0
0.5
0
10
20
30
40
50
60
70
DAYS


4
GONADAL INDEX
7
6
5
4
3
2
0
10
20
30
40
50
60
70
DAYS


5
LN OF DRY WEIGHT OF GLAND (mg)
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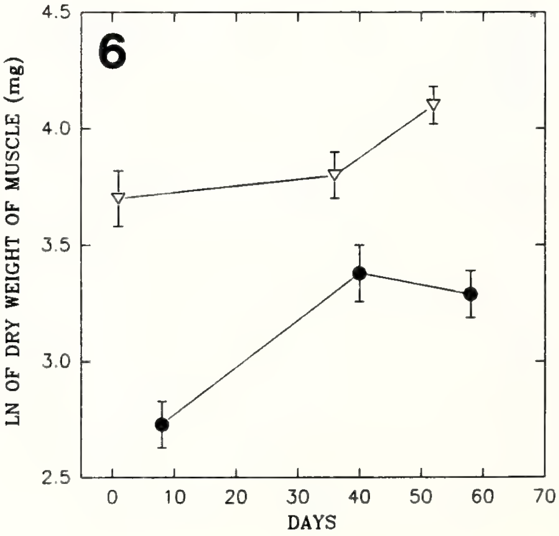
3.00
2.75
2.50
0
10
20
30
40
50
60
70
DAYS


6
LN OF DRY WEIGHT OF MUSCLE (mg)
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3.0
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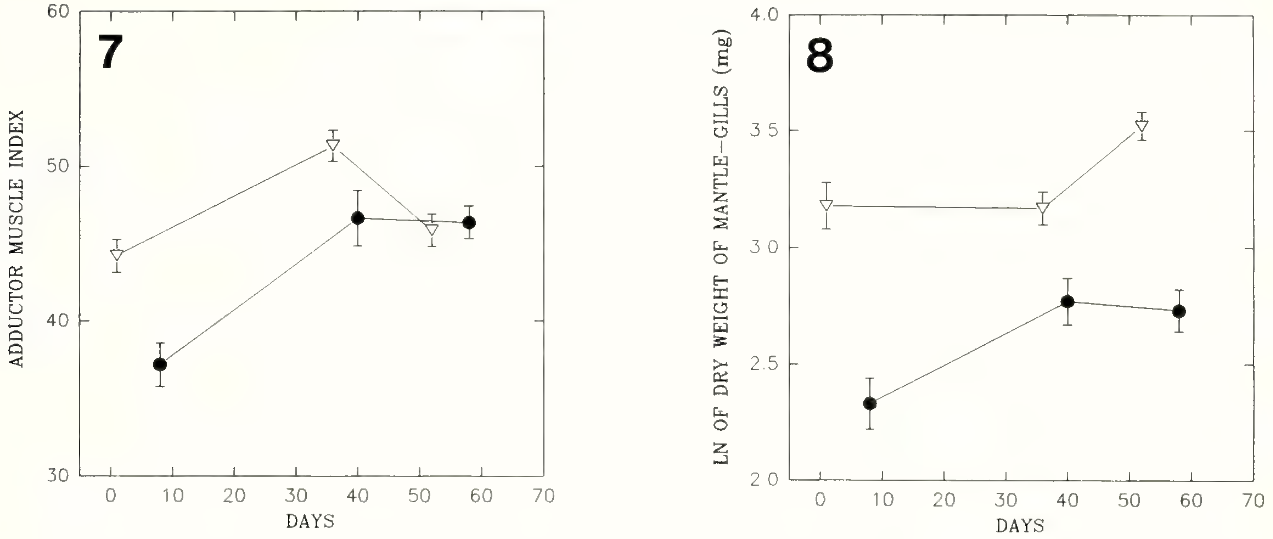
10
20
30
40
50
60
70
DAYS



Figs. 1-8. Comparison of morphometric parameters over time in eight- and 16-month-old *Argopecten ventricosus* in the laboratory. **Fig. 1.** Shell height. **Fig. 2.** Total weight (natural logarithm). **Fig. 3.** Gonadal dry weight (natural logarithm). **Fig. 4.** Gonadal index. **Fig. 5.** Digestive gland dry weight (natural logarithm). **Fig. 6.** Adductor muscle dry weight (natural logarithm). **Fig. 7.** Adductor muscle index. **Fig. 8.** Mantle-gill dry weight (natural logarithm). All symbols as in Fig. 1.

DISCUSSION

According to Félix-Pico (1991), the size of *Argopecten ventricosus* at reproductive maturity is uncertain. However, Tripp-Quezada (1985) reported initial spawning of *A. ventricosus* at an age of six months. Blake (1972) noted that a minmum age had to be reached before cytoplasmatic growth of oocytes could be initiated. This implies that eight-month-old scallops in my experiment had reached a sufficient age to start gametogenesis.

The gonadal index of eight- and 16-month-old scallops declined during the first 40 days of the experiment. Also, a significant decline in carbohydrate content was observed in the digestive gland and adductor muscle. This could suggest energy was used either for somatic tissue and/or reproduction. I assume some of these carbohydrates were used for reproduction, but were not transferred directly to the gonad before day 40. After day 40, these stored carbohydrates were transformed into gonadal lipids. Several authors have suggested a conversion of pre-stored glycogen into lipids (Gabbott, 1975; Barber and Blake, 1985b).

There were increases in dry weight and protein content of adductor muscle during the first 40 days of the experiment, then declines were observed around day 55 in dry weight and protein content of the adductor muscle. Simultaneously, around day 55, eight- and 16-month-old scallops showed noticeable increases in gonadal dry weight and protein content. Barber and Blake (1985a) considered the adductor muscle in *Argopecten irradians* a long-term storage organ to support vitellogenesis and spawning. I suggest the adductor muscle of *A. ventricosus* stores protein during the first 40 days, then protein catabolism in the adductor muscle supports reproductive activity of the gonad. I observed a similar pattern of storing proteins in the adductor muscle in both eight- and 16-month-old *A. ventricosus.* This similarity in reproductive strategy in both age classes differs from the condition observed in *A. purpuratus* by Martínez (1991), in which the seasonal cycle of adductor muscle protein was significantly different among different size classes. I conclude that the energy metabolism in *A. ventricosus* is similar in eight- and 16-month-old individuals with respect to gametogenesis.

The protein content in the mantle was higher in eight- than in 16-month-old scallops, an indentical situation reported by Martínez (1991) for different age classes of *Argopecten purpuratus.* She suggested this organ stored energy to be used for growth rather than reproduction. This suggests that mantle-gill protein can provide better support for somatic growth in eight- than in 16-month-old tropical scallops.

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An apparent hybrid zone between freshwater gastropod species *Elimia livescens* and *E. virginica* (Gastropoda: Pleuroceridae)

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Abstract. The purpose of this study was to determine evidence for genetic hybridization between sympatric populations of the pleurocerids *Elimia livescens* (Menke, 1830) and *E. virginica* (Say, 1817) in New York state, U.S.A. *E. livescens*, an Interior Basin species, was once totally isolated from *E. virginica*, an Atlantic Slope species, by the Alleghenian Divide during glaciation.

Populations of *Elimia livescens* and *E. virginica* from three different regions across New York were compared on the basis of allozyme genetics involving 22 loci and 39 alleles. *E. livescens* and *E. virginica* collected from regions of allopatry, had alternatively fixed alleles at eight of the 22 loci analyzed. Genetic differentiation was found at 11 of the 22 loci. Nei's genetic distance (D) was 0.322 between the two species in the allopatric regions. There were no significant genetic differences between the populations of each species within a particular region. However, there were significantly higher levels of heterozygosity for both species in a narrow region of sympatry than in the allopatric regions. Despite substantial genetic differences between these two species, seven of the 22 loci indicate evidence for hybridization and introgression occurring in the zone of contact. Because these species existed in allopatry at the peak of glaciation (and prior to opening of the Erie Canal) we feel these differences cannot be explained by differentiation along a continuous gradient of populations.

Freshwater gastropods of the genus *Elimia* [= *Goniobasis*, according to Burch (1989)] have been of considerable interest in recent years to evolutionary biologists because of their extensive endemic radiation in the southeastern United States (Chambers, 1978, 1980, 1982; Dillon and Davis, 1980; Dillon, 1984). The low levels of heterozygosity and gene flow among these populations are believed to be primarily caused by rare events of dispersal by *Elimia* between drainage basins (Chambers, 1982; Dillon, 1984). The genetic divergence among these isolated populations also appears to be related to gene flow restriction created by physical barriers (*e.g.* rivers, dams) (Dillon, 1984). In fact, the amount of divergence among these populations of *Elimia* is greater than that reported for *Drosophila* by Ayala *et al.* (1974). Despite the extensive amount of work on the radiation of *Elimia* spp. in the southeastern United States, virtually nothing is known about the genetics of *Elimia* populations in other regions.

In the northeastern United States, populations of *Elimia livescens* (Menke, 1830), an Interior Basin species, were totally isolated from *E. virginica* (Say, 1817), an Atlantic Slope species, by the Alleghenian Divide during Wisconsinan and perhaps earlier episodes of glaciation (Ortmann, 1913; Strayer, 1987). Contact between these species has now been established as a consequence of a dispersal route created by the opening of the Erie Canal in 1825; it is possible but not likely that such contact was initiated ca. 13,000 years B.P. with the Mohawk River outlet of the Great Lakes (Strayer, 1987). Immigration routes such as this can act to reduce the amount of differentiation among conspecific populations because of enhanced gene flow or even allow congeners to hybridize. As examples, it has been demonstrated that the opening of the Erie Canal has resulted in hybridization within both bivalve genera *Anodonta* and *Lampsilis* (Bivalvia: Unionidae) (Kat, 1986).

The purpose of this study was to determine the genetic variability among northeastern populations of *Elimia livescens* and *E. virginica* in regions of sympatry and allopatry. We will also present evidence for genetic hybridization between these two species in the zone of contact in central New York state.

MATERIALS AND METHODS

Animals and Localities. Seven populations of *Elimia livescens* and *E. virginica* were sampled in three different regions of New York state from Buffalo southeast to Ulster County (Fig. 1). Shell morphology is very distinct between *E. livescens* and *E. virginica* (Fig. 2). Identifications at the

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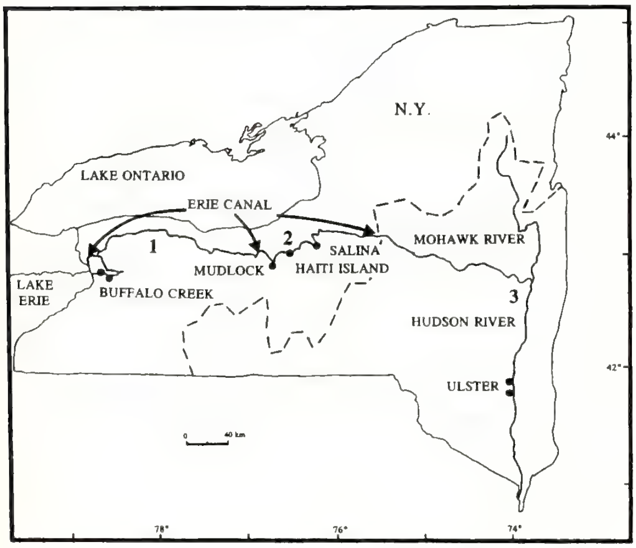

Fig. 1. Map of New York state, showing drainage systems and locations (solid circles) where populations of *Elimia virginica* and *E. livescens* were sampled. Dashed line indicates the drainage divide between St. Lawrence and Atlantic Basins.

species level were made on the basis of shell phenotype. Region 1 contains allopatric populations of *E. livescens*, region 3 contains allopatric populations of *E. virginica*, and region 2 contains both species in sympatry (Fig. 1). In the region of sympatry there was a blurring of shell phenotypes between the species and the distinction between the morphotypes was less clear. Snails with *E. virginica*-type shells dominated in Haiti Island, and *E. livescens*-type shells dominated in Salina. In the Mudlock site there was a greater phenotypic mixture and we sorted the snails into two groups: 1) those most resembling the *E. livescens*-type with some shells appearing to be pure *E. livescens*; 2) those most resembling the *E. virginica*-type with some shells appearing to be pure *E. virginica*. As an outgroup for comparative purposes an additional *E. virginica* population was sampled at an outer geographic region on the Potomac River in Harpers Ferry, West Virginia (approximately 500 km from the Ulster location).

Electrophoresis. Snails were shipped live to the Academy of Natural Sciences of Philadelphia (ANSP), where they were frozen at -70°C in tissue buffer. Specimens to be analyzed using electrophoresis were hand-ground in a small amount (5-10 µl) of deionized water. The shells were not removed, however, they were scrubbed clean to remove any additional organic material on the surface of the shell before grinding.

Eleven loci served to demonstrate genetic differentiation among populations: AAT-1, APH, EST, GP1, ISDH, LAP, NADD, OCT, 6PGD, PGM, and XDH. Invariant loci were ACPH-1, ACPH-2, AO, FUM, G6PD, MDH-1, MPI, SDH, SOD-1, and SOD-2. There were two loci with populations fixed for alternative alleles (LAP, XDH) and nine loci exhibiting polymorphism (Table 1).

Horizontal starch-gel electrophoresis was carried out using the general methods of Ayala *et al.* (1973) as modified by Dillon and Davis (1980) and Davis *et al.* (1981). Six different buffer systems were used: 1) tris-citrate (TC), pH 6; 2) TC, pH 8; 3) tris-edta-borate (TEB), pH 8; 4) TEB, pH 9.1; 5) TEB, pH 9.1 gel buffer and TEB, pH 8 tray buffer; and 6) TC, pH 8.75 gel buffer and sodium-borate (Poulik), pH 7.6 tray buffer. Starch gels were prepared using 34 g of Electrostarch and 250 ml of gel buffer. Run times for each of the gels and buffers are as reported in Davis *et al.* (1988).

Wicks of No. 3 Whatman filter paper were saturated with supernatant from the homogenized tissue from each individual. They were blotted and applied, one wick from each individual, to be run concurrently. The gels were sliced into three layers for staining. Agar overlays were employed for all enzyme assays except AAT and LAP for which aqueous solutions were used. Standard recipes for all

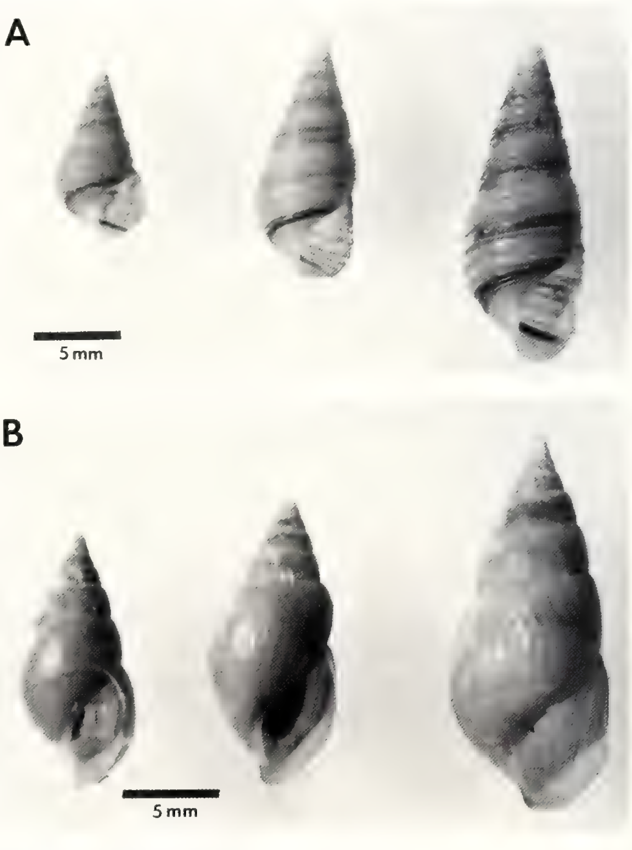

Fig. 2. Representative shells of *Elimia virginica* (A) and *E. livescens* (B) collected from allopatric localities (Ulster and Buffalo Creek, respectively).

Table 1. Allele frequencies from 11 loci (where polymorphism is exhibited at least once) of seven populations of *Elimia* collected along the Erie Canal. Species names are based on shell phenotype. H* = presumed hybridization and introgression. Hybrid group (1) represents *E. livescens* shell phenotype with a trend toward *E. virginica;* hybrid (2) represents *E. virginica* shell phenotype with a trend towards *E. livescens*. (*, diagnostic).

Locus		*E. virginica* Ulster	*E. livescens* H*(1) Mudlock	*E. virginica* H*(2) Mudlock	*E. livescens* Buffalo
ATT-1:	100	1.000	0.097	0.711	–
*	97	–	0.903	0.289	1.000
APH:	100	1.000	1.000	1.000	0.983
	98	–	–	–	0.017
EST:	100	0.979	1.000	1.000	1.000
	98	0.021	–	–	–
GPI:	100	1.000	0.016	0.974	–
*	97	–	0.984	0.025	1.000
ISDH:	100	1.000	–	0.211	0.586
*	98	–	0.042	0.789	0.362
	98	–	0.958	–	0.002
LAP:	100	1.000	–	1.000	–
*	97	–	1.000	–	1.000
NADD:	100	1.000	0.210	0.763	–
*	105	–	0.790	0.237	1.000
OCT:	106	–	–	0.263	–
*	103	–	–	0.079	–
	100	1.000	–	0.632	–
	96	–	0.548	–	0.817
	91	–	0.452	0.026	0.183
6PGD:	100	1.000	–	0.250	–
*	103	–	1.000	0.750	1.000
PGM:	103	–	0.974	0.026	1.000
*	100	1.000	–	0.974	–
	97	–	0.026	–	–
	94	–	–	–	–
XDH:	100	1.000	–	1.000	–
*	98	–	1.000	–	1.000

systems are in Poulik (1957), Brewer (1970), and Shaw and Prasad (1970). The recipe for NADD was developed in the ANSP laboratory in 1982 by Robin Hadlock.

Computations on genetic data were made using a version of NY-SYS (Rohlf *et al.*, 1972) and BIOSYS-1 (Swofford and Selander, 1981). The standard Nei's distance (1978) and the Cavalli-Sforza and Edwards (1967) Arc distance coefficients were calculated and phenograms prepared using the numerical taxonomy program NT-SYS and UPGMA option.

Voucher specimens (two shells of each) from some populations were cataloged into the ANSP collections: *Elimia virginica* from Harpers Ferry (ANSP 373457); *E. virginica* from Ulster County (ANSP 373458); *E. livescens* combined from Cazenovia and Buffalo Creeks (however, only snails from Buffalo Creek were used for electrophoresis). As small samples were taken from Ulster, Salina, and Harpers Ferry, West Virginia, frequency data are not listed here.

Nei's and Arc Genetic Distances. We include data on Nei's genetic distance (D) because it is a standard of long use and thus allows comparisons with the literature. The relative value of Nei's, Rogers', and the Cavalli-Sforza and Edwards' Arc distances have been discussed (Davis *et al.*, 1988). In short, given closely related populations and species, Nei's D will compact values at the lower end of the distance scale. Nei's D is a squared distance value that will rise linearly with time, as more genetic divergence accumulates. There is no upper limit because Nei's D is not metric. The Arc distance is metric and provides a better understanding of relationships from zero similarity (no shared alleles) to 100% identity.

RESULTS

We obtained 22 loci with 39 alleles (Tables 1, 2). There were 11 polymorphic loci of which nine were diagnostic (Table 1). The outgroup for this study was *Elimia virginica* from West Virginia (N = 4). It was monomorphic at all loci and matched the gene frequencies we observed in the Ulster population of this species from the Hudson River. The Ulster population was polymorphic at only one locus. In considering both populations, a mean of 24 individuals was examined from each locus. *E. livescens* from Buffalo Creek was monomorphic at seven (78%) of the nine diagnostic loci.

Table 2. Genetic variability at 22 loci in all populations (standard error in parentheses). (A, allopatric; S, sympatric).

Population	Mean sample size per locus	Mean no. of alleles per locus	Polymorphic loci (%)	Mean heterozygosity (direct count)
Elimia virginica, West Virginia (A)	4.0 (0.0)	1.0 (0.0)	0	0
E. virginica, Ulster (A)	20.4 (1.0)	1.0 (0.0)	0.5	0.002
E. livescens, Buffalo Creek (A)	25.8 (1.4)	1.2 (0.1)	13.6	0.014
E. virginica, Haiti Isl. (S)	6.0 (0.0)	1.0 (0.0)	4.5	0.015
E. virginica, Mudlock (S)	18.9 (0.0)	1.4 (0.2)	31.8	0.044
E. livescens, Salina (S)	5.0 (0.0)	1.2 (0.1)	18.2	0.035
E. livescens, Mudlock (S)	29.0 (1.0)	1.3 (0.1)	27.3	0.050

Nei's D was 0.332 between the outgroup *Elimia virginica* and Buffalo Creek *E. livescens*; Arc distance was 0.577. The two distance values between the two populations of pure *E. virginica* were 0 and 0.020, respectively. The numbers are adequate for determining genetic distance. As discussed in Davis (1983), genetic distances are not much affected by sample size. To gain a more refined estimate of genetic distance between two species than that based on only two individuals necessitates the use of 30 or more individuals (Sarich, 1977). A sample of two individuals will yield a heterozygosity (H) within 2.5% of that calculated from a much larger sample size; there is less than 0.1 difference in D (Gormon and Renzi, 1979).

Emphasis in this report is placed on examining what is occurring at Mudlock; it is clear that hybridization and introgression are evident. There are no F1 generation snails involved as there is fixation for alternative alleles at the LAP locus. However, evidence for introgression is found at seven (78%) of the diagnostic loci. Most striking are data for the individuals considered to be hybrids that graded to pure *Elimia virginica.* At the 6PGD locus there was a frequency of 0.750 for the *E. livescens* alleles; at the NADD locus this was 0.237, and 0.289 at the ATT locus. A significant amount of *E. virginica* alleles was found in individuals that were suspected of being hybrids with shell characters grading to pure *E. livescens* only at the AAT-1 and NADD loci.

As shown in Table 2, the lowest heterozygosity was in the West Virginia population of *Elimia virginica* (H = 0) followed by the Ulster populations of *E. virginica* (H = 0.002); the control *E. livescens* population had an H of 0.014. Hybridization at the Mudlock groupings was indicated by H values of over three times that found for control *E. livescens* (*i.e* 0.044 or 0.050) (Table 2).

Deviation from Hardy-Weinberg expectations was encountered at one locus (ISDH) of the *Elimia livescens* population from Buffalo Creek. There was a pronounced deficiency of the 100/98 heterozygotes. While the number of snails used from Mudlock classified as *E. virginica* or hybrids had a mean of 18.9 per locus, there was a clear trend for heterozygote deficiency at AAT-1, NADD, OCT and 6PGD. Increasing sample size would probably not eliminate these deficiencies.

DISCUSSION

We acknowledge the two greatest weaknesses of the study: 1) on the basis of shells there was no exact method to differentiate populations of hybrids from "pure" parental types; and 2) there were insufficient individuals to preserve phenotypic classes (*i.e.* it was impossible to remove animals for extraction of enzymes without destroying the shells) to voucher the choices we made in selecting the hybrid groupings at Mudlock.

GENETIC DISTANCE AND HETEROZYGOSITY

This study brings to 11 the number of *Elimia* species studied in terms of allozyme population genetics. Chambers (1980) studied *E. vanhyningiana* (Goodrich, 1921), *E. floridensis* (Reeve, 1860), *E. athearni* (Clench and Turner, 1956), *E. albanyensis* (Lea, 1864), *E. curvicostata* (Reeve, 1861), and *E. dickinsoni* (Clench and Turner, 1956) from Florida. Dillon and Davis (1980) studied *E. proxima* (Say, 1825), *E. simplex* (Say, 1825), and *E. semicarinata* (Say, 1829) from Virginia and North Carolina.

There are some interesting patterns that surface when analyzing mean genetic distances and mean heterozygosities between *Elimia* species in data provided by three studies (Chambers, 1980; Dillon and Davis, 1980; Dillon, 1988): 1) species pairs have Nei's distances averaging from 0.33-0.59 (standard deviations range from 0.33-0.99); 2) conspecific populations can have relatively large mean differences (0.12-0.15; Chambers, 1980; Dillon and Davis, 1980), however, those observed in this study were quite low; and 3) mean heterozygosity is very low (0.01-0.08). As Dillon and Davis (1980) pointed out, there is considerable fixation of alternative alleles both between and among conspecifics. The implication for conspecifics is that gene flow between populations of the same species or species complex is probably very low, even within the same drainage system. Because of these general observations and the very low levels of heterozygosity among populations of all northern species thus studied, the situation along the Erie Canal stands out prominently. Although this study is preliminary, the collective evidence indicates the first case of hybridization and introgression within the Pleuroceridae.

HYBRID ZONES

Very few examples of hybrid zones between molluscan species have been reported. The greatest in-depth analyses involve marine bivalves of the genus *Mytilus* [see extensive review and study, Vainola and Huilsom (1991)]. Other examples involve land snail genera such as *Cepaea* and *Cerion* [reviewed by Barton and Hewitt (1985)], unionid clams of the genera *Anodonta* and *Lampsilis* (Kat, 1986), and *Mercenaria* (Dillon and Manzi, 1989; Dillon, 1992).

The zone of *Elimia* species overlap in New York is, as thus far known, relatively narrow, < 40 km. The width of many hybrid zones is typically considerably larger than the dispersal for the individual organism, implying that neutral diffusion is occurring for genes that control the traits being observed (Hewitt, 1988). The dispersal rate for these *Elimia* species in this region is not known. As is characteristic of hybrid zones, polymorphism increases (increased mean heterozygosity), hybrizymes increase, and heterozygote deficiency is frequently observed. In this study we feel there is evidence for introgression of *E. virginica* genes into the western-most population investigated, *i.e.* Buffalo Creek *E. livescens*, considering the seven diagnostic loci that show no overlap between allopatric populations of *E. livescens* and *E. virginica.*

Snails from Salina (N = 5) matched gene frequencies for *Elimia livescens* at most loci but showed some allelic overlap with *E. virginica* at AAT-1:100 and NADD:100 (*E. livescens* was fixed at allele 97 at those two loci) indicating some introgression. Results at the ISDH locus also suggest introgression as ISDH:96 had a high frequency in the Salina and Mudlock *E. livescens*; this allele was not found in *E. virginica.* This allele was at low frequency in Buffalo *E. livescens*, a population that also had ISDH:98, not seen in West Virginia or Ulster *E. virginica* but seen in the populations at Mudlock and Salina. Several interpretations are possible. The ISDH:100 allele could be a shared primitive allele; the ISDH:96 allele could have recently evolved in mid-state *E. livescens* or as a hybrizyme. Overall, given the very low heterozygosity found in general in species of *Elimia*, and the mixture of alleles at the ISDH locus for Salina, Mudlock, and Buffalo snails, the data suggest that introgression is occurring.

Vainola and Huilsom (1991) very effectively showed the occurrence of a hybrid zone in *Mytilus* populations, however, their diagnostic loci were not nearly as distinct as the allopatric populations when compared to this study. Although we were not able to show statistical significance of heterozygote deficiency of snails in the contact zone (Mudlock station), the magnitude of the difference is considerably more than that seen among some hybrid populations of *Mytilus*. The appearance of a novel polymorphic locus (PGM) at Haiti Island, not found in either of the allopatric populations of *E. livescens* or *E. virginica* may seem peculiar. However, this pattern, although not well understood, has been observed in other hybrid zones; in particular Woodruff and Gould (1980) observed this in *Cerion* populations.

The age of this zone is probably very recent, with contact of Interior Basin *Elimia livescens* with northeastern slope *E. virginica* made possible by the opening of the Erie Canal in 1825. The detection of this hybrid zone should be of considerable interest to students of speciation, especially given the genetic structures of *Elimia* populations. Local populations within a drainage system are often highly differentiated genetically; gene flow is evidently slow. In a transplantation experiment mixing conspecific populations of *E. proxima* with fixed different alleles at one or two loci, introduced genes spread at 15-20 m upstream and 5-10 downstream per year (Dillon, 1988). In some cases the progress of hybridization, which can result in fusion, extinction, or speciation, can actually occur at a rate of one gene at a time (Bert and Harrison, 1988).

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Research Note

Morphological differences between zebra and quagga mussel spermatozoa

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Abstract: Sperm morphology of the zebra mussel, *Dreissena polymorpha* (Pallas, 1771), and of the currently-unnamed quagga mussel are described from light and scanning electron microscopy. Differences in shape of the sperm head and acrosome are described as a potentially useful tool in distinguishing the two species.

There are currently two species of dreissenid mussels that have invaded North America. The appearance of the first species, *Dreissena polymorpha* (Pallas, 1771), was described by Hebert *et al.* in 1989. A description of a second species, whose identity is not known but which is currently called the quagga mussel, was made by May and Marsden in 1992**. In addition to genetic differences, the two species differ in shell morphology (Pathy and Mackie, 1993). The quagga mussel lacks the acute angle or carina between the ventral and dorsal surfaces of the zebra mussel shell. This difference in shell morphology can be difficult to discern in some mussels, especially to those who examine mussels only occasionally. The difference in sperm morphology described in this note could be helpful in the positive distinction between male zebra and quagga mussels.

As a part of an ongoing study of the reproductive cycle of zebra mussels, samples of quagga mussels were also examined to determine if there were differences in the reproductive patterns of the two species. Upon examination of fixed and stained soft tissues of mussels under light microscopy, it became apparent that there were clear and consistent differences in gross morphology of the spermatozoa. Examination of simple squash preparations of small amounts of viscera from live specimens revealed that differentiation between males of the two species was possible without extensive sample preparation. To examine the morphological differences more closely, zebra and quagga mussel spermatozoa were examined by scanning electron microscopy.

The mussels examined were collected on 22 July 1993 from the Black Rock Lock adjacent to the Niagara River in Buffalo, New York. Both zebra and quagga mussels were found at the same site. For electron microscopy, squashes of a small portion of the visceral mass from several individuals of each species were made for quick determination of sex. The remaining tissues were fixed for two hours at 7°C in 2.5% glutaraldehyde and 0.1 M cacodylic acid, pH 7.2. Tissues were then washed three times in 0.1 M cacodylate buffer followed by 2% osmium tetroxide solution for ten minutes each. The samples were dehydrat-

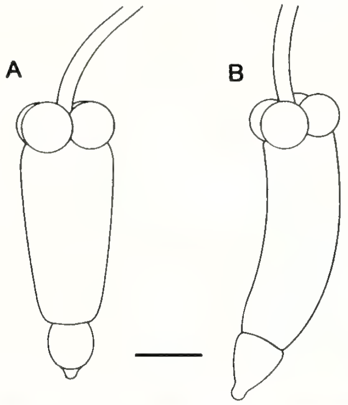

Fig. 1. Comparison of the spermatozoan morphology of zebra mussel (A) and quagga mussel (B). Scale = 1 µm.

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**The quagga mussel has since been identified as *Dreissena bugonsis* Andrusov, 1897, by G. Rosenberg and M. L. Ludyanskiy, and A. P. Spidle, J. E. Marsden and B. May in two publications to appear in volume 51 of the *Canadian Journal of Fisheries and Aquatic Sciences.*

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ed stepwise in a series of solutions containing 50, 60, 75, 90 and 100% ethanol. Tissues were dried in a critical point dryer before being coated with gold under an argon atmosphere. The prepared samples were examined using an Electroscan environmental scanning electron microscope.

The sperm heads of zebra mussels are straight, short, and blunt, whereas those of the quagga mussel are curved, longer, and more pointed, somewhat reminiscent of a scaphopod shell (Fig. 1). The difference in morphology is apparent even in an unstained squash preparation under relatively low magnification (400X). Electron photomicrographs show the described differences clearly (Figs. 2 -3).

Measurements using electron photomicrographs revealed that the mean length of *Dreissena polymorpha* sperm heads is 4.0 ± 0.1 µm (N = 5), whereas that of quagga mussels is 4.7 ± 0.2 µm (N = 7). Mean width of zebra mussel sperm at the widest point is 1.6 ± 0.1 µm (N = 4), as compared to 1.3 ± 0.1 µm (N = 4) in quagga mussels. The zebra mussel sperm head is more bulbous in appearance than that of the quagga mussel sperm, which has a more sharply pointed outline. Again, the most distinguishing feature is the straight, short appearance of zebra mussel sperm in contrast to the curved, longer appearance of quagga mussel sperm.

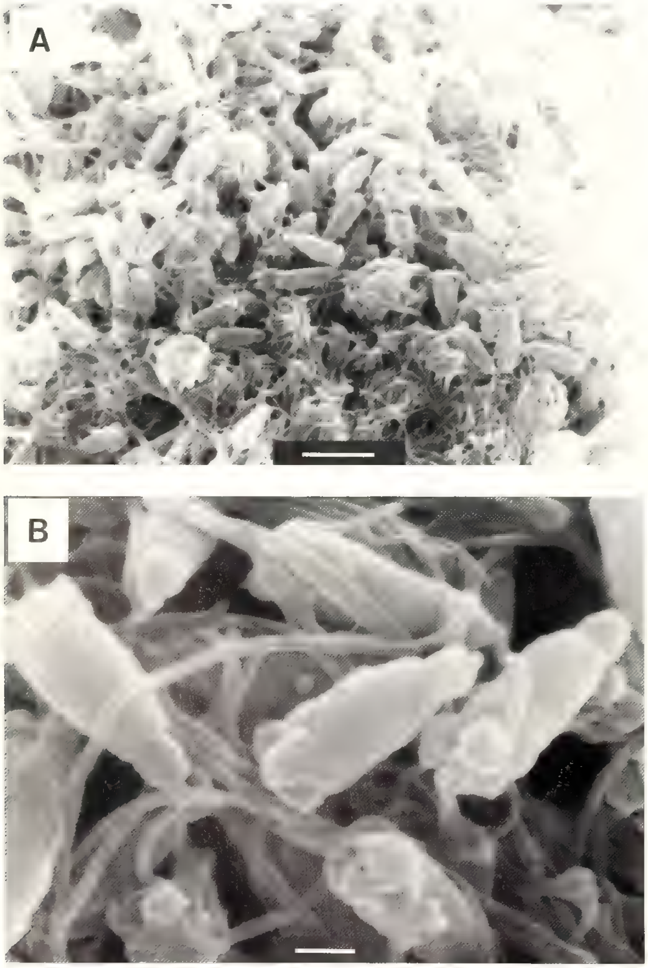

Fig. 2. Scanning electron photomicrographs of the spermatozoa of zebra mussels. Scale = 5 µm (A), 1 µm (B).

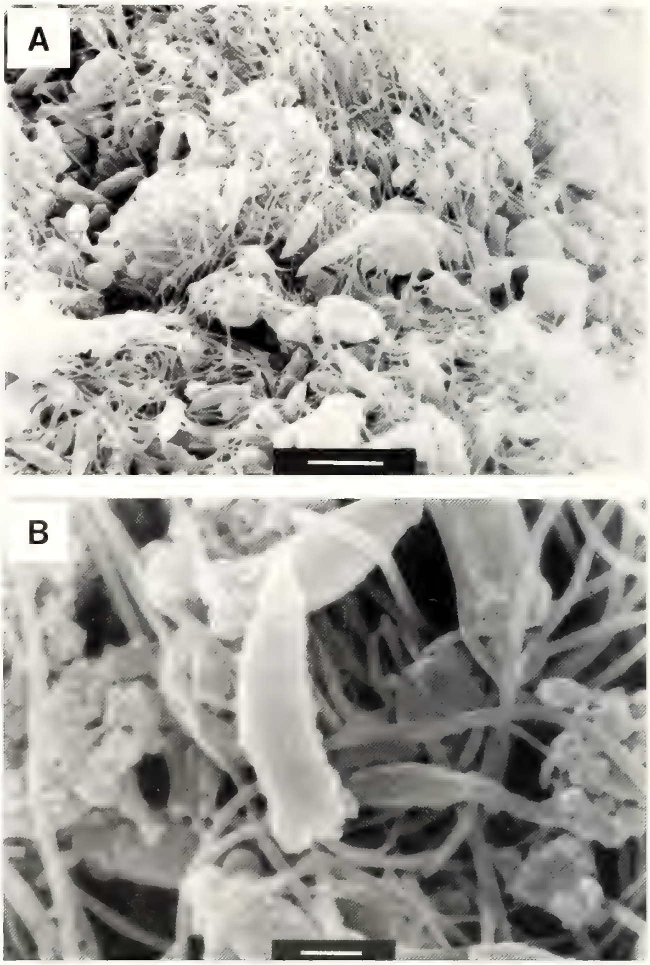

Fig. 3. Scanning electron photomicrographs of the spermatozoa of quagga mussels. Scale = 5 µm (A), 1 µm (B).

Differences are also apparent between the acrosomes of the two sperm types. In the zebra mussel, the acrosome is more bulbous and oval in shape than that of the quagga mussel. In the latter species, the acrosome is wide at the point of attachment to the rest of the sperm head, but tapers more sharply toward the tip. In both types, the primary acrosome vesicle is visible as a small nib at the apex of the acrosome. This structure is functionally important, as its membrane covering disarticulates at fertilization to fuse with the plasma membrane of the ovum (Dan, 1970).

Spermatozoa of both zebra and quagga mussels possess elongated flagella, which are at least several times the length of the head portion. Flagella of the sperm of both species project from the broad base of the head, and this junction is surrounded by four rounded structures which contain mitochondria (Mackie, 1984).

Sperm morphology has been used as a tool in the study of systematic zoology by a number of workers. Such investigations have included oligochaetes (Jamieson, 1984), ascidians (Franzen, 1992), and rodents (Roldan *et al.*, 1992). In addition, similar studies of gastropod spermatozoa have been employed in the examination of congeneric limpets (Hodgson and Bernard, 1988; Jamieson *et al.*, 1991).

With regard to mussels, if positive distinction between the two species of *Dreissena* based on shell morphology is not possible, the described differences in the appearance of the sperm could be helpful. Of course, the usefulness of this technique is limited to male mussels, and only to that part of the reproductive cycle during which sperm are present, generally between March and September.

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AMERICAN MALACOLOGICAL UNION
FINANCIAL REPORT

General Accounts

INFLOWS		
Membership Dues		11004.00
1992	65.00	
1993	9410.00	
1994	1529.00	
Life Membership		450.00
Bulletin Sales		630.50
Subscriptions (Vol. 10)	291.00	
Subscriptions (Vol. 11)	222.00	
Back Issues & Suppliments	117.50	
Sales of Other Publications		809.92
Recovered Publishing Costs		4576.60
Page Charges	3125.00	
Reprints	1451.60	
Donations		607.00
Symposium Fund	357.00	
Student Award	250.00	
Interest (Bank Accounts)		1796.25
Miscellaneous Income		78.24
FROM Symposium Endowment Bond Fund (Interest)		37.62
FROM Symposium Endowment Stock Fund (Interest)		106.90
TOTAL INFLOWS		20097.03
OUTFLOWS		
Office Expenses		897.96
Telephone/Postage	545.75	
Printing	201.09	
Miscellaneous	151.12	
Bank Charges		301.28
Dues in Other Organizations		230.00
Incorporation Fees		20.00
Insurance/Bond		391.00
Accounting Fees		250.00
Publication Costs		12819.58
Bulletin 10(1)	9056.37	
AMU News 23(3), 24(1) & 24(2)	3763.21	
Travel Expenses		1500.00
Symposium Speakers		1500.00
Student Paper Awards		750.00
TO Symposium Endowment Bond Fund		14150.00
TO Symposium Endowment Stock Fund		21222.41
TO Life Membership Endowment Stock Fund		4950.00
TOTAL OUTFLOWS		58982.23
NET CASH FLOW		(38885.20)
CASH BALANCE (1/1/93)		95132.91
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61st ANNUAL MEETING
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HILO, HAWAII
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Hillis, D. M. 1989. Genetic consequences of partial self fertilization on population of *Liguus fasciatus* (Mollusca: Pulmonata: Bulimulidae). *American Malacological Bulletin* 7(1):7-12.

Seed, R. 1980. Shell growth and form in the Bivalvia. *In: Skeletal Growth of Aquatic Organisms,* D. C. Rhoads and R. A. Lutz, eds. pp. 23-67. Plenum Press, New York.

Yonge, C. M. and T. E. Thompson. 1976. *Living Marine Molluscs.* William Collins Son & Co., Ltd., London. 288 pp.

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Larval and juvenile shells of four North Atlantic scaphopod species

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Abstract. Ontogenetically early shells of four North Atlantic scaphopod species, *Antalis occidentalis* Stimpson, 1851, *Entalina quinquangularis* (Forbes, 1844), *Pulsellum lofotensis* (M. Sars, 1865), and *Cadulus subfusiformis* (M. Sars, 1865) were examined by SEM. The larval shell of previously described scaphopods can be divided into the bulbous protoconch A and the more or less elongated protoconch B. In *A. occidentalis* and *E. quinquangularis*, a smooth teleoconch A is distinguished from the ribbed teleoconch B. The protoconch of *A. occidentalis* matches previous reports on *A. tarentinum* (Lamarck, 1818) (type 1). *E. quinquangularis* and *P. lofotensis* have a protoconch with a marked constriction, but without annulations (type 2). In *C. subfusifomis*, only teleoconchs A and B were found, but no distinct protoconchs. Teleoconch A of this species resembles a juvenile *Pulsellum*, before it forms a constriction separating it from the rapidly expanding teleoconch B. In addition to shell morphometrics, the microstructure is described for each species. The results are compared to earlier descriptions of Recent and fossil scaphopod protoconchs: type 1 is restricted to the Dentaliida, type 2 typical for Gadilida except for the presumably derived condition in *C. subfusifomis*.

The first to describe and figure larval shells of the dentaliid scaphopods *Antalis dentalis* (Linné, 1766) and *A. entalis* (Linné, 1758) were Lacaze-Duthiers (1856-1857) and Kowalevsky (1883). Sars (1865) gave the first report of a gadilid larval shell, *Entalina quinquangularis* (Forbes, 1844). Since then scaphopod larval shells have been occasionally reported (Table 1), but mostly as by-products of other investigations. Scarabino (1979) noted differences between the orders regarding larval shells: Dentaliida have several annulations, Gadilida only one. The minute larval structures are also preserved in fossils; MacNeil and Dockery (1984), Ruggieri (1987) and Engeser *et al.* (1993) described lower Jurassic to Pliocene specimens.

The major difficulty in the study of early scaphopod shell development is the dynamics of the mantle-shell morphology. The posterior mantle margin starts to dissolve or decollate the tip of the shell soon after metamorphosis so as to maintain an apical shell aperture large enough for the increasing respiratory needs (Lacaze-Duthiers, 1856-1857; Steiner, 1991; Reynolds, 1992). Although the onset of this shell-destructing process seems to vary between species (Engeser *et al.*, 1993), the larval shell is lost in all but very young specimens, and various stages of erosion may be seen.

Engeser *et al.* (1993) sketched a general outline of a scaphopod larval shell. Based upon this concept and the reports in the literature (Table 1), the outline of a dentaliid larval shell in Fig. 1 serves as morphological reference for the species examined in this paper. The larval shell or protoconch shows two structurally different regions. The earliest part of the shell is a bilaterally symmetrical, saddle- or clasp-shaped secretion that is not fused ventrally (Bandel, 1982). Engeser *et al.* (1993) coined the name "genae" for this bulging part of the shell; here it is termed protoconch A. The younger part of the larval shell, protoconch B, extends both posterior and anterior to protoconch A. The posterior part is the chimney-like fumarium (Engeser *et al.*, 1993); the anterior one shows the characteristic annulations, followed by a short cylindrical region at the transition

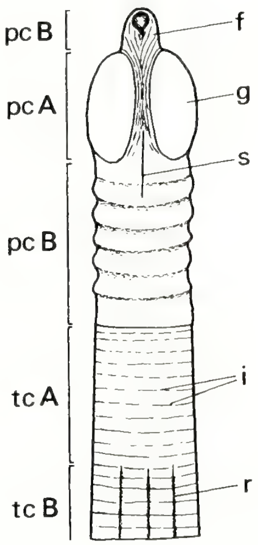

Fig. 1. General outline of dentaliid larval shell, ventral view; modified after Engeser *et al.* (1993). (f, fumarium; g, genae; i, increment lines; pc A, protoconch A; pc B, protoconch B; r, ribs; s, suture; tc A, teleoconch A; tc B, teleoconch B).

Table 1. Larval shells of Recent (r) and fossil (f) scaphopods previously described and/or illustrated (*).

DENTALIIDA			
Antalis tarentinum (Lamarck, 1818)	Lacaze-Duthiers, 1856-1857	r	*
	Bandel, 1982	r	*
	Engeser *et al.*, 1993	r	*
Antalis cf. *dentalis* (Linné, 1766)	Kowalevsky, 1883	r	*
Antalis sp. "A"	Scarabino, 1979	r	*
Antalis cf. *pseudofissura* Janssen, 1978	Engeser *et al.*, 1993	f	*
Fissidentalium phaneum (Dall, 1895)	Burch and Burch, 1989	r	
Fissidentalium jaffaensis Cotton and Ludbrook, 1938	Cotton and Godfrey, 1940	r	*
Fissidentalium laqueatum (Verrill, 1885)	Henderson, 1920	r	
Dentalium sp.	Engeser *et al.*, 1993	f	*
"Dentalium" zephyrinum Casey, 1903	MacNeil and Dockery, 1984	f	*
"Dentalium" polygonuum Casey, 1903	MacNeil and Dockery, 1984	f	*
"Dentalium rectum" Gmelin, 1790	Ruggieri, 1987	f	*
Episiphon hyperhemileuron (Verco, 1911)	Cotton and Godfrey, 1940	r	*
GADILIDA			
Entalina quinquangularis (Forbes, 1844)	Sars, 1965	r	*
Entalinopsis callithrix (Dall, 1889)	Scarabino, 1979	r	*
Entalinopsis sp.	Engeser *et al.*, 1993	f	*
Heteroschismoides subterfissum (Jeffreys, 1877)	Davies, 1987	r	*
"Laevidentalium" sp.	Engeser *et al.*, 1993	f	*
Suevidontus jaegeri Engeser, Riedel and Bandel, 1993	Engeser *et al.*, 1993	f	*
Baltodentalium weitschati Engeser and Riedel, 1992	Engeser *et al.*, 1993	f	*
Gadila turgida (Meyer, 1886)	Engeser *et al.*, 1993	f	*

to the teleoconch. There is a suture marking the line of ventral mantle and shell fusion extending from between the bulging sides of protoconch A onto protoconch B. In many scaphopods with longitudinal sculpture, the teleoconch has two or three sections. The early adult shell, teleoconch A, lacks ribs or striae and shows transverse growth lines only. The ribbed part is teleoconch B. In the genus *Antalis*, for example, a third section, teleoconch C, is differentiated, where the longitudinal ribs have faded and the shell is smooth again. The letters "A" and "B" are preferred to numbers to avoid confusion or inadequate homologization with prodissoconch sequences of gastropods and bivalves. Only one (see Discussion) of the dentaliid species studied has a constriction at the anterior end of protoconch B as figured by Engeser *et al.* (1993). Therefore, such a constriction is not part of the common dentaliid pattern.

The only report on early shell development in the family Gadilidae is that on the fossil *Gadila turgida* by Engeser *et al.* (1993). The larval shell, being somewhat bell-shaped, lacking a fumarium, and having "The suture and the genae ... only poorly developed" (Engeser *et al.*, 1993:90), has only little resemblance with the pattern outlined above. The larval and juvenile shells of four North Atlantic species of Scaphopoda are described and morphometrically characterized in this paper. Three of them have not been described previously. Sars' (1865) description of the larval shell of *Entalina quinquangularis* is updated.

MATERIAL AND METHODS

Antalis occidentalis Stimpson, 1851, *Entalina quinquangularis*, *Pulsellum lofotensis* (M. Sars, 1865), and *Cadulus subfusiformis* (M. Sars, 1865) were collected off Saksvik, Trondheimfjord, Norway (63° 27'N, 10° 32'E) from 100-238 m depth, using a benthic sled with 1 mm mesh size. The sediment was carefully washed through a 250 µm nylon net, the animals sorted under a binocular microscope and preserved in 70% ethanol. All specimens used in this study were collected at this site or at other locations in Trondheimfjord. Juvenile specimens of *C. subfusiformis* as described in this paper were also found in Raunefjord near Bergen. For scanning electron microscopy (SEM), the samples were transferred to absolute ethanol prior to air-drying, mounted, sputter-coated, and examined with a Jeol-JMS 09 scanning electron microscope.

Morphometric measurements were taken as indicated in Fig. 2 from SEM photomicrographs. Lengths of the total shell, protoconch (and its components protoconch A and protoconch B), teleoconch, and, if present, teleoconch A and teleoconch B, were measured. Shell diameters were taken at the apical aperture, maximum width of protoconch A (which is in all cases the maximum diameter of the entire protoconch), initial width of the teleoconch (identical with the terminal diameter of the protoconch), basal aperture, and, if present, width at the transition from teleoconch A to

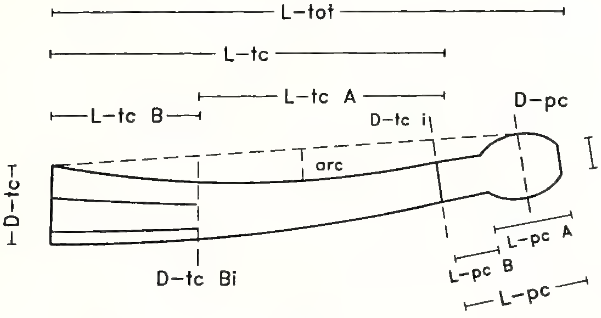

Fig. 2. Diagram of shell measurements. (D-ap, apical diameter; D-pc, maximum protoconch diameter; D-tc, maximum teleoconch diameter; D-tc Bi, initial teleoconch B diameter; D-tc i, initial teleoconch diameter; L-pc, length of protoconch; L-pc A, length of protoconch A; L-pc B, length of protoconch B; L-tc, total length of teleoconch; L-tc A, length teleoconch A; L-tc B, length of teleoconch B; L-tot, total length).

teleoconch B. An additional measurement in *Cadulus subfusiformis* was the maximum diameter of teleoconch A, because it is not identical with the initial diameter of teleoconch B. A common measurement for curvature is the arc, the maximum normal distance between the shell and the line between anterior and posterior dorsal shell margins (Ludbrook, 1960). The length:width ratio of the protoconch was calculated from its total length and the maximum diameter. The coefficients of variation (CV; %) were calculated (standard deviation/mean x 100) to provide a unit- and dimension-free indicator of the variability of each parameter (Zar, 1984). Their comparison beyond that in variability profiles seemed not appropriate, because there is no test of significance for the CV of more than two characters (Sokal and Braumann, 1980) and not all measures are of the same dimensionality (Lande, 1977). Principal Component Analysis (PCA) based on the variance/convariance matrix of log-transformed data was accomplished using Statgraphics Plus ver. 5.2 (Graphic Software Systems, Inc.). Of the program's output, only Eigenvalues and the weights for each measurement on each axis were used. The principal components were calculated using the equation

$$Y_i = (x_1 - X'_1) \times w_{i1} + (x_2 - X'_2) \times w_{i2} + \ldots + (x_i - X'_i) \times w_{ii}$$

where Y_i is the principal component of the i-th axis, x the measurement, X' the global mean, and w the weight of the measurement on the i-th axis (Johnson and Wichern, 1988). I preferred not to use other standardizations of the log-transformed data to maintain the mutual positions of the data points. This ensures that, using the global means and weights given in Table 3, morphometric data of other specimens can be plotted onto the resulting diagrams, and thus compared with those of the present study.

RESULTS

SHELL MORPHOLOGY

Antalis occidentalis

The five juvenile specimens found with the larval shell still attached ranged from 1.49-3.43 mm in length (Table 2) and showed various stages of apical erosion (Fig. 3). The larval shell fits the general dentaliid pattern. Its mean length is 465 ± 61 µm, the length:width ratio (L:W) is 2.62. The protoconch diameter provided the least variable measure. In contrast to all other protoconch parameters (variability 14.78-19.31%), it varied by only 4.68% (Table 2).

Several growth lines separated the smooth and bulging sides of protoconch A from the suture (Fig. 3G). The fumarium was more or less eroded in all specimens; therefore, both the orientation and the width of the apical shell orifice varied. Protoconch B had five to seven annulations. The transition from protoconch B to teleoconch A is straight or almost so (Figs. 3A-E). Although the diameter of protoconch A is slightly larger than that of protoconch B, there is no constriction. Teleoconch A is smooth with the exception of growth lines and about 1.8 mm long. Anteriorly, the longitudinal ribs of teleoconch B appear.

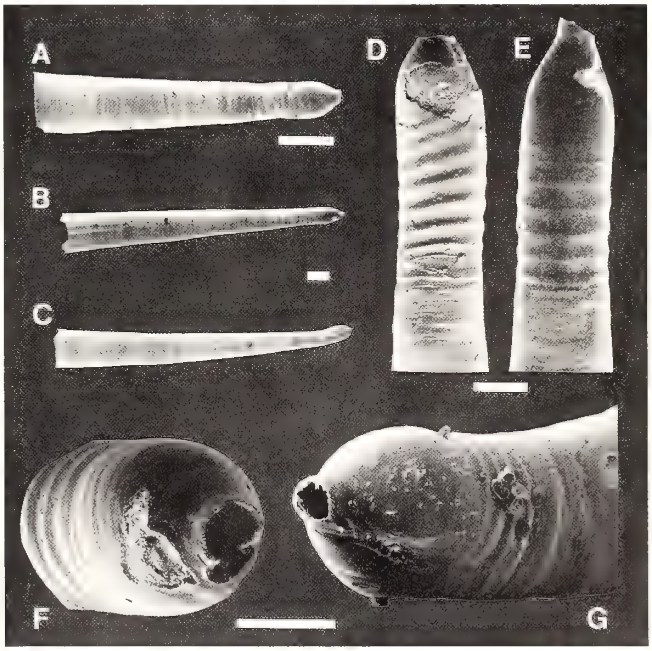

Fig. 3. Larval and juvenile shells of *Antalis occidentalis*. **A.** Smallest specimen in lateral view; teleoconch B is not developed yet. **B-C.** Dorsal (B) and lateral (C) view of specimens with teleoconch B, the latter being the only one with protoconch and teleoconch forming an angle. **D.** Larval shell with fumarium almost eroded. **E-F.** Detail of B showing the widened apical shell opening. **G.** Ventral view of A showing the well developed protoconch A (genae) and the suture extending onto protoconch B. Scale bars = 100 µm.

Table 2. Means (± S.D.) of shell measurements in µm. [Abbreviations as in Fig. 2; also, CV = coefficient of variation expressed as percent (S.D. x 100 / mean), D-tc A = maximum teleoconch A diameter (*Cadulus subfusiformis* only), L:W = protoconch length:width ratio,]. N = 5 *(Antalis occidentalis)*, 15 *(Entalina quinquangularis)*, 11 *(Pulsellum lofotensis)*, and 52 *(Cadulus subfusiformis)*.

Species	*Antalis occidentalis*		*Entalina quinquanqularis*		*Pulsellum lofotensis*		*Cadulus subfusiformis*	
	Mean	CV	Mean	CV	Mean	CV	Mean	CV
A. Total Shell Measurements								
L-tot	2583 ± 709	27.46	1612 ± 347	21.52	951 ± 192	20.18	1182 ± 99	8.39
D-ap	67 ± 11	16.78	53 ± 26	49.47	77 ± 17	21.85	163 ± 31	18.88
D-tc	379 ± 60	15.91	310 ± 63	20.30	229 ± 63	27.51	328 ± 152	46.21
arc	51 ± 22	42.63	177 ± 52	29.18	59 ± 20	33.76	64 ± 26	40.63
B. Protoconch Measurements								
L-pc	465 ± 69	14.78	264 ± 31	11.59	205 ± 29	13.99	—	—
L-pc A	186 ± 29	15.86	183 ± 12	6.71	122 ± 28	23.23	—	—
L-pc B	279 ± 54	19.31	81 ± 26	31.99	83 ± 17	20.86	—	—
D-pc A	178 ± 8	4.68	108 ± 4	3.38	109 ± 4	3.53	—	—
L:W	2.62 ± 0.39	14.80	2.43 ± 0.27	10.92	1.89 ± 0.28	14.77	—	—
C. Teleoconch Measurements								
L-tc	2118 ± 650	30.70	1345 ± 357	26.56	748 ± 205	27.44	—	—
Teleoconch A								
L-tc A	1387 ± 306	22.07	545 ± 124	22.82	—	—	802 ± 226	28.12
D-tc i	175 ± 10	5.75	109 ± 6	5.31	109 ± 5	4.80	—	—
D-tc A	—	—	—	—	—	—	236 ± 12	5.21
Teleoconch B								
L-tc B	732 ± 377	51.48	532 ± 298	56.02	—	—	376 ± 266	70.59
D-tc Bi	320 ± 35	10.78	211 ± 12	5.71	—	—	208 ± 18	8.56

Among teleoconch parameters, the initial diameters of teleoconch A and B were most invariable (CV 5.14% and 9.64, respectively; Table 2), but the variability of teleoconch A length (19.74%) was about average.

Entalina quinquangularis

The 15 specimens with larval shells ranged from 1.07-2.34 mm long; the larval shells measured about 264 ± 30 µm in length, with L:W 2.43. The larval shell is smooth, sometimes with growth lines near the border to teleoconch A (Fig. 4). Protoconch A was less set off from protoconch B than in *Antalis occidentalis* (Figs. 4A, E) and, therefore, the border between them less obvious. It lies in the area where the larval shell starts to decrease in diameter. The ventral midline is marked by a distinct suture. The fumarium is short, smooth, and eroded in most specimens. Protoconch B forms a constriction, beyond which the shell increases abruptly in diameter forming a conspicuous annulus preceeding the youngest part of protoconch B. A slight angle is formed either by the protoconch constriction or by the axes of the proto- and teleoconch. Like in *A. occidentalis,* there is a typical teleoconch A with growth lines only (Figs. 3A-C). The five characteristic ribs of the species' teleoconch B become visible about 0.8 mm from the larval shell. The circular anterior shell opening then becomes more and more pentagonal.

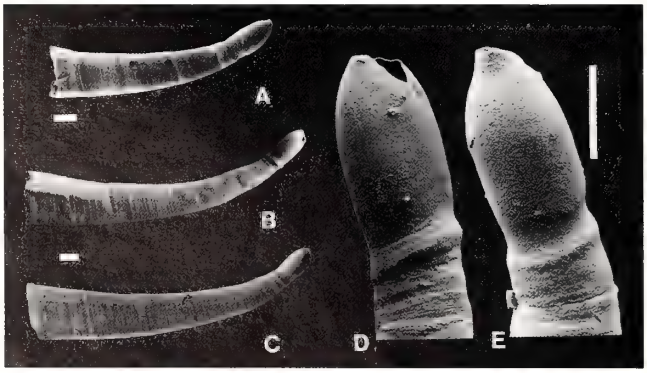

Fig. 4. Larval and juvenile shells of *Entalina quinquangularis.* **A-C.** Lateral views of entire specimens. **D.** Detail of B showing the widened apical opening and the suture. **E.** Specimen with the most clearly distinguishable protoconch A and fumarium. Scale bars = 100 µm.

Pulsellum lofotensis

The 11 specimens of *Pulsellum lofotensis* with almost complete larval shells ranged from 0.64-1.21 mm in length; the mean protoconch length was 205 ± 27 µm, with L:W 1.89. Generally, the protoconch resembles that of *Entalina quinquangularis.* It is, however, significantly shorter and stouter in shape (Fig. 5), as the lower L:W expresses (see below). The larval shell has a more rounded

Table 3. Principal Component Analysis: Eigenvalues, global means of measurements [log(gl-x)] and their weights (w) for each Principal Component (PC I-X). Abbreviations as in Fig. 2.

		PC I	PC II	PC III	PC IV	PC V	PC VI	PC VII	PC VIII	PC IX	PCX
Eigenvalue		0.1288	0.1147	0.0301	0.0099	0.0065	0.0031	0.0018	0.0006	0.0002	3.28E-5
	log(gl-x)	w	w	w	w	w	w	w	w	w	w
L-tot	3.151	0.4801	-0.0576	0.0747	-0.2083	-0.1744	-0.2212	0.0352	-0.1698	0.0427	0.7784
L-pc	2.409	0.2174	-0.1754	-0.2967	-0.0080	0.4955	0.0926	0.7610	0.0070	-0.0180	-0.0154
L-tc	3.056	0.5323	-0.0228	0.1497	-0.2606	-0.2977	-0.2526	0.1153	-0.2544	0.1093	-0.6193
D-pc	2.069	0.1142	-0.1921	-0.0163	-0.1953	-0.0452	-0.1528	-0.0621	0.3890	-0.8533	-0.0544
D-ap	1.776	-0.0621	-0.1658	0.7914	0.0212	0.5297	-0.2400	-0.0270	-0.0536	0.0017	-0.0043
D-tc i	2.070	0.1149	-0.1823	-0.0103	-0.1473	-0.0155	-0.1573	-0.0474	0.8123	0.4943	-0.0187
D-tc	2.441	0.3007	-0.0179	0.2978	-0.2024	-0.0054	0.8736	-0.0802	0.0978	-0.0210	0.0037
L-pc A	2.194	0.2013	0.0392	-0.3931	-0.3414	0.5718	-0.0436	-0.5710	-0.1538	0.0572	-0.0700
L-pc B	1.984	0.3254	-0.5876	-0.1028	0.6802	-0.0157	0.0525	-0.2577	-0.0653	0.0054	-0.0438
arc	1.972	0.4147	0.7216	0.0585	0.4562	0.1590	-0.0719	-0.0241	0.2342	-0.0987	-0.0131
% total variance		43.54	38.78	10.19	3.36	2.20	1.05	0.60	0.19	0.07	0.01

appearance: protoconch A is not clearly demarcated from protoconch B and a suture is not evident. All specimens show at least slight signs of apical erosion or truncation (Fig. 5), and so the presence of a fumarium cannot be confirmed. In most shells, the transition from the constriction of protoconch B to the annulus is not as abrupt as in *E. quinquangularis*. The cylindrical section of protoconch B bordering the teleoconch is similar to that of other scaphopods. Because there are only growth lines and no longitudinal sculpture, teleoconchs A and B can not be distinguished. The anterior opening of the teleoconch is circular.

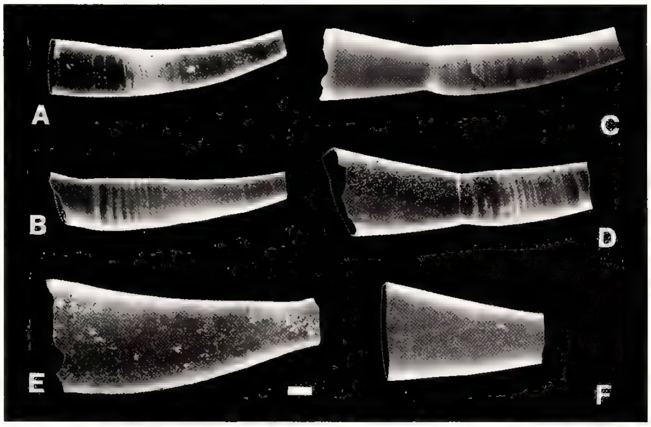

Fig. 6. Juvenile shells of *Cadulus subfusiformis*. **A-B.** Teleoconch A. **C-D.** Eroding teleoconch A and commencing teleoconch B. **E-F.** Incomplete, stub-like teleoconchs B; teleoconch A eroded. Scale bar = 100 μm.

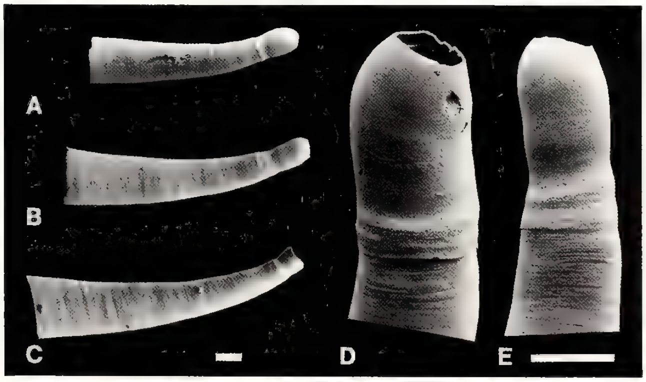

Fig. 5. Larval and juvenile shells of *Pulsellum lofotensis*. **A.** Complete protoconch. **B.** Onset of apical erosion. **C.** Half of protoconch eroded. **D.** Lateroventral view of protoconch with widened apical opening. **E.** Detail of B, showing the different surface textures of protoconch and teleoconch. Scale bars = 100 μm.

Cadulus subfusiformis

Bulbous larval shells like those described above have not been found in this species. Instead, aberrant looking scaphopods with somewhat trumpet-like shells (Fig. 6) turned out to be juvenile *Cadulus subfusiformis*, showing the typical radula morphology of the species. The apical part of the shell, teleoconch A, is a slowly expanding tube, like the teleoconch of *Pulsellum lofotensis* but almost straight. Then, after a short constricted section, a rapidly expanding teleoconch B is formed. The length of these trumpet-like shells varied little (0.89-1.39 mm; mean 1.18 ± 0.1 mm; N = 52; see also Table 2), but the relative proportion of the two sections does, indicating well synchronized anterior secretion and posterior truncation processes. Animals which have not yet started to secrete teleoconch B are very similar to juvenile *P. lofotensis*, but can be identified by their slightly depressed anterior shell opening. The shell surface is always smooth, without any longitudinal sculpture. Faint growth lines are present on teleoconch A; teleoconch B lacks even those. Surface texture of teleoconch B is amorphous and completely smooth under SEM

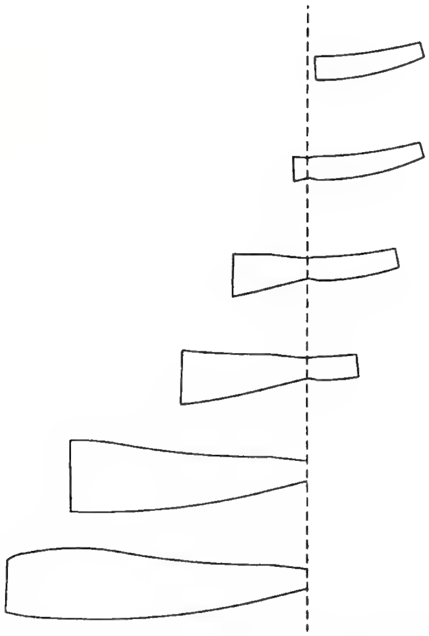

Fig. 7. Shell growth series of juvenile *Cadulus subfusiformis* (diagrammatic).

(Fig. 6C), but that of teleoconch A is crystalline. About 44% of the specimens (23 of 52) have an area where the early crystalline texture alternates with the amorphous teleoconch texture on teleoconch A. Thus, a series of annulations are seen under SEM (Figs. 6A, B, D).

Occasionally, I found stub-like, incomplete teleoconchs of *Cadulus subfusiformis* without the typical anterior constriction (Figs. 6E, F). From the various shapes and stages of the trumpet-like and stub-like shells, a growth series can be inferred (Fig. 7).

SHELL MICROSTRUCTURE

The shells of all species examined have a layer of prismatic crystals, the only component of the most recently secreted shell parts (Fig. 8A). In the older portions, the prismatic layer is lined by a crossed lamellar layer. Close to its outer border, the lamellae are slightly irregular. The first-order lamellae are perpendicular to the long axis of the shell and, in juvenile specimens, form an angle of about 45° with the shell diameter (Fig. 8B). In adult specimens, the lamellae become almost tangential to the internal shell lumen. A distinct layer of organic material outside the calcareous ones (periostracum) was evident only in three specimens of *Cadulus subfusiformis*, but was definitely lacking in the other species examined.

The prismatic shell layer in *Antalis occidentalis* was 2.0-2.3 µm thick near the anterior shell edge, but up to 3 µm in the fumarium (Fig. 8A). In *Entalina quinquangularis*, the prisms were 1.7-2.3 µm high (Fig. 8C), those of *Pulsellum lofotensis* were between 1.3 and 1.8 µm (Figs. 8B, D, E). Compared to the other species, the crossed lamellar layer in *E. quinquangularis* rapidly increases in thickness behind the anterior shell edge. The shell thus quickly gains strength and stability, but only slowly increases in internal diameter. *Cadulus subfusiformis* has an outer prismatic layer 1.3-2.0 µm thick. In the apical portions of teleoconch A, the prisms have rounded tops with pits between them, but those of teleoconch B fit tightly together, each giving rise to the respective surface texture (see above). Being formed by the outer prismatic layer only, the incomplete definitive teleoconch is extremely thin and fragile, so that manipulation and transport often damaged the shell edge. When the teleoconch is completed,

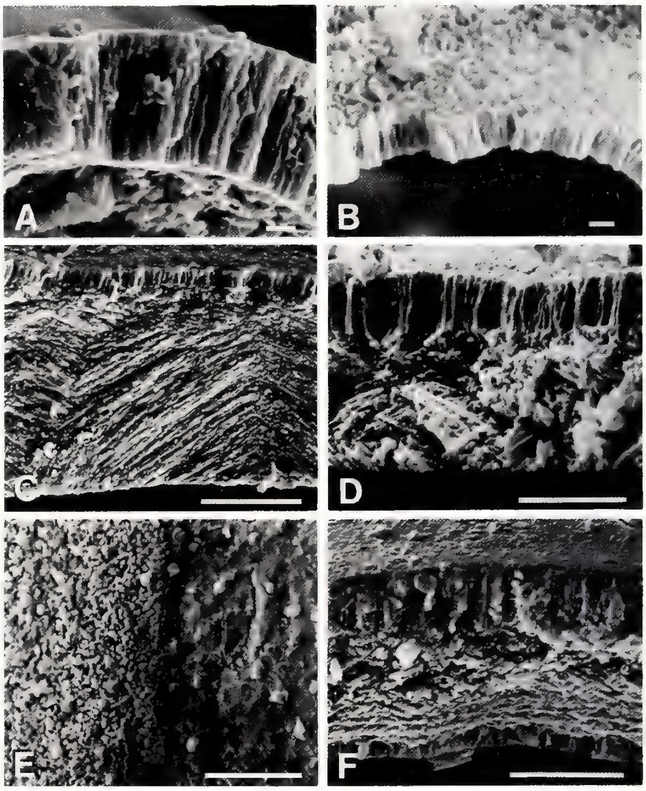

Fig. 8. Shell microstructure: **A.** *Antalis occidentalis;* prismatic layer at the fumarium margin (apical part of protoconch B). **B.** *Pulsellum lofotensis;* prismatic layer at the apical margin of protoconch A. **C.** *Entalina quinquangularis*; transversal fracture of early teleoconch B, prismatic and thick cross-lamellate layers. **D.** *Pulsellum lofotensis;* transversal fracture of early teleoconch, prismatic and cross-lamellate layers. **E.** *Pulsellum lofotensis;* change in shell surface texture at the transition from protoconch (left) to teleoconch (right). **F.** *Cadulus subfusiformis;* transversal fracture of early teleoconch B; outer prismatic and cross-lamellate layers lined by flat inner prismatic layer. Scale bars = 1 µm (A-B); 5 µm (D-F); 10 µm (C).

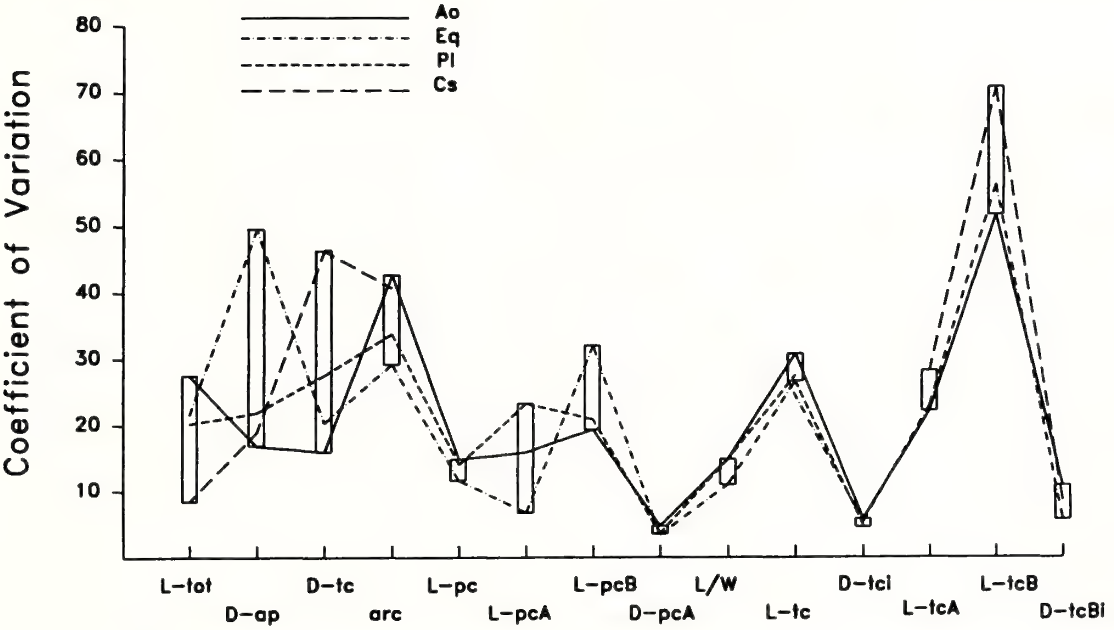

Fig. 9. Variability profiles of 14 characters for *Antalis occidentalis* (Ao) *Entalina quinquangularis* (Eq), *Pulsellum lofotensis* (Pl) and *Cadulus subfusiformis* (Cs). The vertical bars indicate the range of CV for each character for all species, taken from Table 2. Abbreviations of characters as in Fig. 2.

however, it is multi-layered, very tough and resistant to fracture. The mature shell is comprised of the outer prismatic layer, the crossed lamellar layer, each about 2 µm thick, and a 0.5-1 µm thin inner prismatic layer (Fig. 8F).

MORPHOMETRIC ANALYSIS

The coefficients of variation (CV) for 14 shell measurements of each species (as listed in Table 2) are plotted as variability profiles in Fig. 9. For *Cadulus subfusiformis*, only teleoconch measurements were available. The three most invariable characters for all species were the maximum diameter of the protoconch (D-pc A) and the diameter at the transitions from proto- to teleoconch (D-tc i) and from teleoconch A to B (D-tc Bi, missing in *Pulsellum lofotensis*). The length of teleoconch B, when present, was the most variable character. Congruency between profiles was high on the right side of L-pcB, where some protoconch and the teleoconch characters were plotted. It was lowest for the total shell measurements.

Ten length and diameter measurements of total shell, protoconch and teleoconch, of *Antalis occidentalis, Entalina quinquangularis* and *Pulsellum lofotensis* were used for Principal Component Analysis (PCA). The measurements of teleoconchs A and B (missing in *P. lofotensis*) and the data of *Cadulus subfusiformis* (protoconch not known) were excluded. Eigenvalues, weights and global means of each measurement are listed in Table 3. The first two axes (PC I and II) of the PCA represent 82.33%, the first three, 92.52% of total variance. The plotted PC I and II (Fig. 10A) clearly separated *A. occidentalis* from the two gadilid species that were close to each other but did not overlap. In the plot of PC I and III (Fig. 10B), however, *E. quinquangularis* and *P. lofotensis* separated more clearly, while the former overlapped considerably with *A. occidentalis*.

PC I was mainly a length axis: all characters except for D-ap were loaded positively, L-tc and L-tot having the highest loads (= weights). PC II reflected the inverse relative correlation of arc and some protoconch measurements: *A. occidentalis* having the longest protoconch B was almost straight, but the gadilid species with a low L-pc B value were more curved. The other negatively loaded characters on PC II were D-pc, D-tc i and L-pc. Positive loads on the diameters of the shell apertures (D-ap, D-tc) and negative loads on protoconch length (L-pc A, L-pc) determined PC III, indicating that with increasing teleoconch diameter, protoconch A became shorter, in relative and absolute terms, and its aperture larger (see Discussion). In addition, linear regressions were drawn for each species (Fig. 10).

The principal components of log-transformed measurements of the juvenile shells described and listed by Engeser *et al.* (1993) were similarly calculated. The results are plotted in Fig. 10C.

Significant differences between the L:W ratio of *Entalina quinquangularis* and *Pulsellum lofotensis* were demonstrated by a STUDENT t-test for equal variances. The t-statistic of 4.95 with 23 D.F. was significant at $\alpha = 0.001$ to reject H0 (no differences in means).

DISCUSSION

The previously reported scaphopod larval and juvenile shells (Table 1) and those described above present three different types (Fig. 11). The first and best-known type has a bulging, very distinct protoconch A, a long protoconch B with three to nine annulations, and no constriction at the border to the teleoconch (Fig. 11A). It is reported from four species of the genus *Antalis*, three species of *Fissidentalium*, *Episiphon hyperhemileuron,* and four presumably dentaliid species of questionable generic position. In the second type, protoconch A is less clearly distinguishable from protoconch B than is often the case in the type 1 larval shell. Protoconch B is comparatively short and forms a constriction and a subsequent marked annulus bordering the teleoconch (Fig. 11B, C). This type of protoconch is known from four species of the genera *Entalina*, *Entalinopsis* and *Heteroschismoides* belonging to the gadilid suborder Entalimorpha, the gadilimorph genus *Pulsellum,* and from three species of uncertain systematic position ("*Laevidentalium*" sp., *Baltodentalium weitschati,*

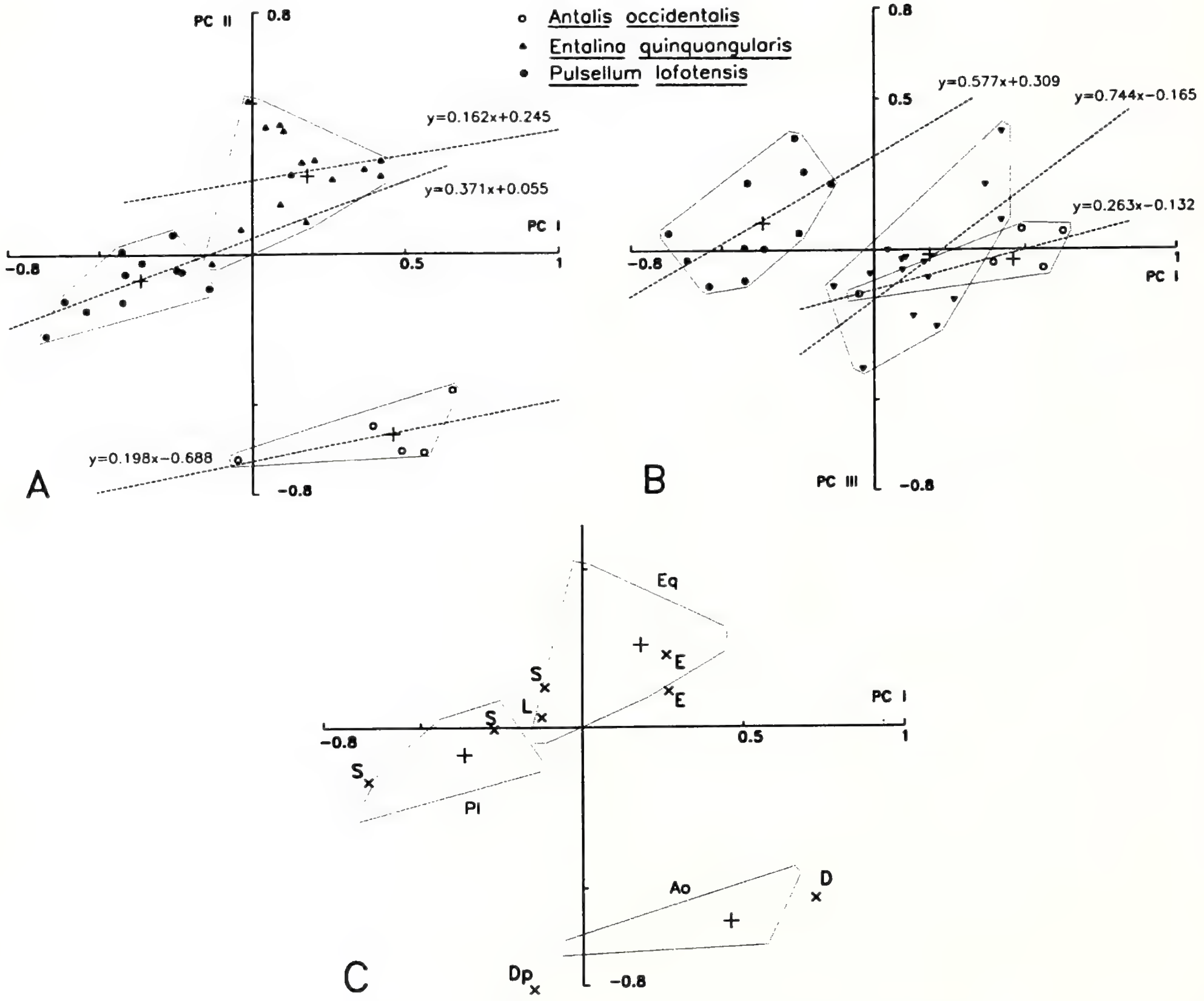

Fig. 10. Plots of Principal Component Analysis of ten characters of *Antalis occidentalis, Entalina quinquangularis* and *Pulsellum lofotensis* (see text). **A.** Plot of PC I and II. **B.** Plot of PC I and III. Linear regression equations are given as $y = kx + d$. **C.** Plot of PC I and II showing the species areas as in A (crosses indicating means) and the fossil specimens from Engeser *et al.* (1993). (Ao, *Antalis occidentalis;* D, *Dentalium* sp.; Dp, *Dentalium pseudofissura*; E, *Entalinopsis* sp.; Eq, *Entalina quinquangularis*; L, *"Laevidentalium"* sp.; Pl, *Pulsellum lofotensis*; S, *Suevidontus jaegeri).*

Suevidontus jaegeri).

Cadulus subfusiformis and the confamiliar, paleocenic *Gadila turgida* differ from both these types: there is no trace of a clasp-like or bulbous protoconch and, in *C. subfusiformis,* there is a constriction between teleoconch A and B (Fig. 11D). Instead, *G. turgida* has a bell-shaped protoconch (Engeser *et al.,* 1993) that is not similar to those of other scaphopods. The shell development of *C. subfusiformis* resembles that of *G. turgida* in having transverse annulations in the surface texture of early shell parts and in having an anteriorly constricted teleoconch. However, *G. turgida* lacks the constriction between teleoconch A and B. It seems likely that these closely related species have a similar mode of shell development and perhaps the same type of protoconch. Only ontogenetic studies will reveal whether such a bell-shaped larval shell also exists in *C. subfusiformis.* Besides complete lack in ontogeny, several reasons may account for the absence of a protoconch in this material of *C. subfusiformis*: loss in the course of washing and sorting, very early truncation, or lack of calcification. The juvenile shell described for *C. subfusiformis* definitely is a teleoconch, because the animals found within these shells were unequivocally adult in their organization without even remnants of larval features (*e.g.* a ciliary locomotory organ). The shells were perfectly uniform with the earliest parts already tubular and cylindrical without a trace of a suture. It is by no means certain, however, that teleoconch A of this species is homologous with that of the others described here. *C. subfusiformis* and *G. turgida* obviously represent a third type of early ontogenetic shell morphology, although in the former, no protoconch has yet been found.

The Principle Component Analysis (PCA) is a powerful tool of data reduction to demonstrate and test similarities and differences of complex morphologies. The ten measurements of identical units allowed the use of their variance/covariance matrix. To test the robustness of the dataset, PCA was also performed with the correlation matrix, both with and without adding the L:W ratio to the data. Their results (not shown) were qualitatively identical, indicating that these ten parameters represent a stable dataset. PCA of the protoconch measurements only showed an overlap of *Entalina quinquangularis* and *Pulsellum lofotensis.* Because protoconchs alone are unlikely to be found in sediment samples or collections, I prefer to include the measurements of the early teleoconch in the analysis. As shown in Fig. 10, the juvenile shells of dentaliids and gadilids were clearly separated. This is not only a question of size, although *P. lofotensis* and *Antalis occidentalis* were distinct on principal component (PC) I, mainly a size axis. On the same axis, *E. quinquangularis,* however, overlapped widely with *A. occidentalis.* The latter was separated from the gadilid species on PC II, demonstrating the inverse correlation of arc and length of protoconch B. The distinction between *E. quinquangularis* and *P. lofotensis* was mainly on PC I. In the plot of PC I/III (Fig. 10B), the separation of these two species became clearer: the smaller *P. lofotensis* has a wider apical aperture (D-ap) than the longer *E. quinquangularis*, but a smaller anterior aperture and a shorter protoconch.

The slope of the linear regressions for each species can be used as an indicator of isometric growth of measurements loaded on the PCs when it is approximately 1, as in Fig. 10B for *Pulsellum lofotensis* and *Entalina quinquangularis.* In this case, apical and anterior aperture increased (log-) proportionally with length, but protoconch length, especially that of protoconch A, decreased.

Table 3 provides all parameters to reproduce PCA calculations for data of additional specimens of these and of other species using the given equation. The positions of the two *"Dentalium"* specimens of Engeser *et al.* (1993) in the PCI-PCII-plot (Fig. 10C) grouped with the area occupied by *Antalis occidentalis.* All other specimens showed type-2 protoconch morphology and grouped with *Entalina quinquangularis* and *Pulsellum lofotensis*, supporting the above ordinal assignment. For another fossil larval shell described by Engeser *et al.* (1993), *"Laevidentalium"* sp., this is of particular importance. Generic assignment to *Laevidentalium* refers to the order Dentaliida, but the protoconch with constriction and annulus shows the typical type-2 features of the Gadilida. Although it does not clearly group with *P. lofotensis,* the juvenile shell closely resembles that of *Pulsellum* species I have seen, both in shape and surface sculpture. The protoconch is larger than in *P. lofotensis* but the mean L:W (1.89 ± 0.13, CV = 7.11) calculated from seven specimens listed by Engeser *et al.* (1993) was exactly the same. STUDENT t-tests showed *"Laevidentalium"* to be as different from *E. quinquangularis* as was *P. lofotensis,* with an even higher significance, but not different from *P. lofotensis.* If this species is indeed closely related to the genus *Pulsellum* and can accordingly be grouped within the Pulsellidae, the paleontological record of the family would not begin in the Paleocene but earlier in the middle Jurassic. Origin for the Pulsellidae in this period is in much better accordance with the earliest record of its proposed sister-group, the family Gadilidae (Steiner, 1992) dating from the early Cretaceous (Emerson, 1962).

Comparing the coefficients of variation (CV) (Table 2, Fig. 9), it becomes clear that three measurements are almost constant (CV 3.38-10.78) in all four species. These are all measurements of width: maximum protoconch diameter, and the initial diameters of teleoconch (terminal width of protoconch) and teleoconch B. Although lecithotrophic larvae are definitely known from the genus *Antalis* only (Lacaze-Duthiers, 1856-1857; Kowalevsky, 1883), there is

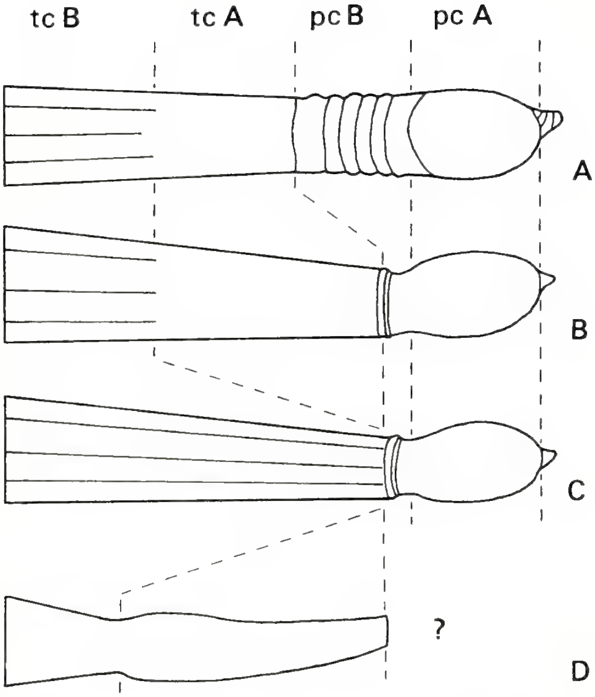

Fig. 11. Comparison of the types of larval and juvenile scaphopod shells. **A.** Dentaliida (*Antalis, Fissidentalium, Episiphon*). **B-C.** Gadilida: Entalimorpha and Gadilimorpha: Pulsellidae (B. *Entalina, Heteroschismoides*; C. *Entalinopsis, Baltodentalium, Suevidontus; Pulsellum* not figured). **D.** *Cadulus subfusiformis* (Gadilida: Gadilimorpha: Gadilidae). (Pa, protoconch A; Pb, protoconch B; Ta, teleoconch A; Tb, teleoconch B).

no indication that *Pusellum lofotensis* and *Cadulus subfusiformis* differ in their development (Steiner, unpubl. obs). The small variability of the maximum and terminal protoconch diameters is probably a consequence of lecithotrophic development with its limited resources of matter and energy. The maximum protoconch diameter is directly correlated with egg diameter, the terminal diameter of the protoconch perhaps only in regard to the limited nutrients (see below). The uniformity of initial teleoconch B diameter, however, is unlikely to be due to the available amount of yolk, unless teleoconch A is secreted prior to the onset of feeding. According to Lacaze-Duthiers (1856-1857), definite mouth and anal openings are present after nine days of development, but he distinguished the adult gut topology only after 30 days because of the opaque yolk remnants. Thus, it is not clear when feeding actually commences. Therefore, it is not impossible that in *Antalis occidentalis* and *Entalina quinquangularis,* teleoconch A is secreted under non-feeding conditions. Although also secreted in the presumed lecithotrophic phase, protoconch length measurements are generally more variable having CVs between 6.71 and 32.99, L-pc B being the least constant. The exception of *Pulsellum lofotensis,* where the CV of L-pc A exceeds that of L-pc B, is explained by the higher number of apically truncated specimens rather than by the variability of the complete shell. If limitation of yolk is the only determining factor for protoconch measurements, why are lengths more variable than diameters? In addition to resource limitation, one can assume genetically fixed, species-specific thresholds in diameter, at which the next growth phase is initiated. Such thresholds may also exist for teleoconch features and appear to be a more plausible explanation of why D-tc Bi is one of the most constant measurements, but L-tc A is not. Another example would be the constriction and subsequent formation of teleoconch B in *C. subfusiformis* after the determined D-tc A of 236 µm is reached.

Apart from already discussed features, *Cadulus subfusiformis* differs from the other species also by its hardly variable total shell length (CV 8.39), while its teleoconch B length has the highest CV (70.59) of all measurements taken in this study. There appears to be a high synchronization of shell growth at the anterior end and shell truncation at the apex. Consequently, teleoconch A of up to 1 mm length is lost before teleoconch B of about 2 mm length is completed.

The available data on larval shell morphology permit a systematic correlation of protoconch types at the ordinal level. Type 1 protoconch is characteristic of the Dentaliida and type 2 of Gadilida except for the genus *Cadulus* that shows type 3. The mode of shell development of *G. turgida* with a weakly differentiated protoconch A may be intermediate between the Gadilida-type and *Cadulus.*

This correlation brings new light to some problems regarding classification of conchological material, particularly fossil scaphopods. Engeser *et al.* (1993) described two fossil species with protoconchs, *Suevidontus jaegeri* and *Baltodentalium weitschati,* but left their family assignment open. According to the morphological and morphometric results presented here, they belong to the order Gadilida. Their type 2 larval shell places them in the order Gadilda, and their conspicuous longitudinal sculpture of teleoconch B is characteristic for some genera of the suborder Entalimorpha like *Entalina* or *Entalinopsis.* Both *S. jaegeri* and *B. weitschati* have a very short (or absent?) teleoconch A resembling *Entalinopsis callithrix* and *Entalinopsis* sp. (Fig. 11C). Although polarities of protoconch character states are far from clear, it is plausible that the short (or absent) teleoconch A is a synapomorphy of these four species and suggests close phylogenetic relationships.

There is little albeit varying information on the teleoconch microstructure of Scaphopoda. Only a brief review of the literature is given here; future investigations will need to cover shell structure comparatively on a broad taxonomic base. One organic and two to four aragonitic layers may be present. A distinct periostracum is reported in recent papers for *Dentalium rectum, Pictodentalium vernedei* (Sowerby, 1860) (*fide* Haas, 1972), and *Antalis vulgaris* (DaCosta, 1778) (= *tarentinum*) (*fide* Alzuria, 1985). This purely organic layer seems to be lacking in *Rhabdus rectius* (Reynolds, 1992) and in all Gadilida examined so far (Shimek and Steiner, in press). This is most surprising in the suborder Gadilimorpha where most of the shells are smooth and lusterous. However, three of the 60+ specimens of *Cadulus subfusiformis* examined in this study had a thin, homogenous, probably organic outer shell layer. Reasons for the lack of the periostracum could be the ethanol preservation or, more likely, early and rapid erosion, because it is also lacking in air-dried shells. The outermost calcareous component is prismatic, with prisms oriented perpendicular to the shell axis (lacking in *R. rectius*). It may rest on a thin amorphous (Shimek and Steiner, in press) or complex crossed lamellar layer (Haas, 1972), followed by an ordinary crossed lamellar layer. Towards the internal lumen, the lamellae may become narrower and more aciculate-like (Haas, 1972; Alzuria, 1985). Especially in the apical teleoconch region, there may be a layer of short prisms perpendicular to the shell axis, a myostracum-like structure. The ontogenetically early shells described above have only one or two layers. The outer prismatic layer is always present. It becomes coated from the inside when the mantle epithelium starts to secrete the crossed lamellar structure. The calcification of the protoconch is believed to take place before (Lacaze-Duthiers, 1856-1857) or at metamorphosis (Engeser *et al.*, 1993). Metamorphosis, however, does not correlate with ventral mantle/shell fusion, which occurs during the secretion of protoconch B. The obliteration of the velum-like larval locomotory organ is a good indicator of the transition to adult organization. It loses its locomotory function as it becomes enclosed by the elongating tubular shell (Lacaze-Duthiers, 1856-1857). The absence of growth lines on the protoconch indicates that it is formed by the shell gland and/or mantle as a purely organic structure and that it calcifies at once (Bandel, 1982; Engeser *et al.*, 1993), as in many Archaeogastropoda and pteriomorph Bivalvia (Bandel, 1982; Waller, 1981). Another similarity to these groups is the *in toto* calcification of the organic protoconch, where the crystals grow from surface to surface, leaving no unmineralized periostracum (Bandel, pers. comm.). This result, in particular, underlines the primitive position of Scaphopoda among the Conchifera in regard to larval development. On the other hand, there are increment lines on the fumarium and the suture indicating their origin as mineralized shell components. Again, we need developmental analyses to decide whether these two structures are added to the shell during or after protoconch secretion and mineralization.

Which type of larval shell represents (or is closer to) the ancestral state is hitherto uncertain. The *Cadulus*-type is probably not the plesiomorphic state, because larval shells with a bulging protoconch A are present in dentaliids and both suborders of gadilids. In addition, form and microstructure of the *Cadulus* teleoconch itself seems to be highly derived. Consequently, the bulging larval shell with a ventral gap found in Dentaliida and both clades of Gadilida is likely to be plesiomorphic. Engeser *et al.* (1993) assumed a longer larval and swimming phase for dentaliids with their longer type-1 protoconch, although there are no signs, whatsoever, that Scaphopoda have planktotrophic larval stages (Engeser *et al.*, 1993; Steiner, unpubl. obs.).

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The relevance of passive dispersal for the biogeography of Caribbean mollusks[1]

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Abstract. Occurrence of teleplanic veliger larvae of sublittoral species in major currents of the tropical Atlantic Ocean supports the hypothesis that passive dispersal of larvae contributes importantly to the biogeography of shoal-water molluscan species. Rafting may play a secondary role. Criticisms of passive larval dispersal as a factor in molluscan biogeography are: (1) that larvae have a fixed life span too short to account for long-distance dispersal: both laboratory and field data show this assertation to be mistaken; (2) that larvae after a time lose their competence to metamorphose: whenever tested, teleplanic larvae have been shown to retain their ability to metamorphose; (3) that dispersal is random and cannot explain congruent nonrandom associations among widely differing taxa: dispersal is largely accounted for by advection along major ocean currents which provide quasi-permanent or seasonally reoccurring corridors for the transport of planktonic larvae; therefore various taxa necessarily are dispersed over similar routes, leading to congruent geographic distributions; and (4) that some species lacking long planktonic larval stages nevertheless have wide geographic ranges and consequently there is little relationship between mode of reproduction and geographic range of species: those species lacking extended planktonic larval stages yet having wide geographic ranges are mostly sessile epibenthic forms that can attach to hard substrata, and consequently are preadapted for passive dispersal by rafting. Dispersal by human agencies also has contributed within historic time to the geographic distribution of marine mollusks. Such alternative modes of dispersal do not negate the importance of larval transport.

Despite demonstrable evidence for widespread passive larval dispersal and in some instances also for the transport by rafting of molluscan species, ecological constraints place restrictions upon where and when new colonists can survive and reproduce.

Geotectonics and sea-floor spreading have been significant in controlling the pattern and extent of passive dispersal over geologic time. The closing of the Tethys Seaway during the Oligocene and Early Miocene resulted in the isolation of the southwestern tropical Pacific Ocean from the Mediterranean Sea and tropical eastern Atlantic Ocean. Similarly, the closing of the corridor between North and South America divided the tropical eastern Pacific Ocean from the Caribbean Sea.

Continental drift and sea-floor spreading resulted in the initial formation and subsequent enlargement of the Atlantic Basin and has led subsequently to the "mid-Atlantic barrier" which today acts as a filter between the tropical eastern Atlantic Ocean and Caribbean Sea. Both tectonic events and sea-floor spreading have placed important constraints on the dispersal between tropical faunas.

Faunal studies of the amphi-Atlantic distributions of marine benthic mollusks further support the hypothesis of passive dispersal. Low endemism on oceanic islands suggests that initial colonization must be largely accomplished by teleplanic larvae. Available evidence shows that although no single process can completely explain the present composition of the Caribbean molluscan fauna, passive dispersal of planktonic veliger larvae must have played and continues to play an important role both in colonization and in maintaining genetic continuity between widely disjunct regions of the tropical Atlantic Ocean.

Recent new techniques now available which reveal enzyme variation and mitochondrial DNA polymorphism can revolutionize the study of biogeography. They can make possible, for example, the identification of closely similar larvae in instances where morphological characteristics are inadequate and can allow measurements of genetic exchange or gene flow and the genetic relationships between widely separated populations. Cladistic analysis, although revealing little about the processes leading to present geographic distributions, can help reconstruct large-scale geographic relationships as related to the evolution of taxa.

"It requires a very unusual mind to undertake analysis of the obvious." A. N. Whitehead.

To understand the origin of the Caribbean sublittoral molluscan fauna requires not only a comparison among spatially disjunct tropical regions throughout the world but also a consideration of the processes, both biologic and geologic, which may have brought about and continue to influence the observed geographic distributions of tropical mollusks. It is not enough simply to make inferences about the origin of existing patterns without explicit evidence for the processes that have been responsible for these observed patterns.

In this paper I will: (1) summarize evidence for passive dispersal of mollusks in Atlantic tropical waters, in particular data on the transport of planktonic larvae and on the rafting of sessile epibenthic species; (2) consider objections that have been raised against such passive dispersal to explain the observed geographic distributions; (3) summarize the relevance of geotectonic events such as the closing of seaways and sea-floor spreading and make inferences about how these geologic processes could have affected passive dispersal and influenced present-day distributional patterns of tropical mollusks, in particular the Caribbean molluscan fauna, and (4) discuss other evidence that suggests that passive long-distance dispersal has and continues to play an important role in the initial colonization and subsequent genetic exchange between widely disjunct populations of Atlantic tropical molluscan species (Scheltema, 1968, 1971b, 1992).

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[1] This review is based on a contribution to the 1992 AMU Symposium on Biology of Caribbean Mollusks. See *American Malacological Bulletin* 10(2):179 ff.

THE ROLE OF PASSIVE DISPERSAL IN ESTABLISHING GEOGRAPHIC DISTRIBUTION OF TROPICAL WESTERN ATLANTIC MOLLUSKS

There are three principal means by which sublittoral mollusks can be passively dispersed, namely: (1) by the transport of their planktonic larvae, (2) by "rafting" on drifting objects, and (3) by the activities of humans within historic time, *i.e.* approximately the past 500 years.

PASSIVE DISPERSAL OF LARVAE

Passive long-distance dispersal of planktonic larvae in tropical waters of the Atlantic Ocean has been the object of continuing studies for more than two decades (Scheltema, 1964, 1968, 1971a, b, 1986; Mileikovsky, 1966; Laursen, 1981). Four principal currents potentially can serve to transport larval forms of tropical sublittoral species over long distances (Fig. 1). The North and South Equatorial Currents (Fig. 1, NEC and SEC) flow from east to west, *i.e.* from West Africa to South America; both are surface currents usually extending no deeper than 50 m. Velocities of the North Equatorial Current have been estimated at 25 to 35 cm/sec, while that of the South Equatorial Current ranges from 25 to 90 cm/sec in some regions. An Equatorial Undercurrent (Fig. 1, EUC) passes from west to east directly beneath the westwardly flowing South Equatorial Current at depths greater than 50 m (Metcalf *et al.*, 1962); its maximum velocity occurs between 50 and 100 m depth and sometimes exceeds 100 cm/sec (Fig. 2). Within the undercurrent, water temperature drops from ca. 26°C at 50 m to 20°C at 100 m. Such temperatures are sufficiently warm to sustain larvae of most tropical mollusks. A fourth current, the Equatorial Countercurrent (Fig. 1, ECC) is found in the region between 5° and 10° N latitude. It is seasonal in its occurrence, flows from west to east toward the coast of West Africa, and is fully developed between June and August when it can attain a velocity greater than 35 cm/sec. (Richardson, 1984). In the fall it diminishes, then disappears completely in January to reappear subsequently in early summer (Fig. 3).

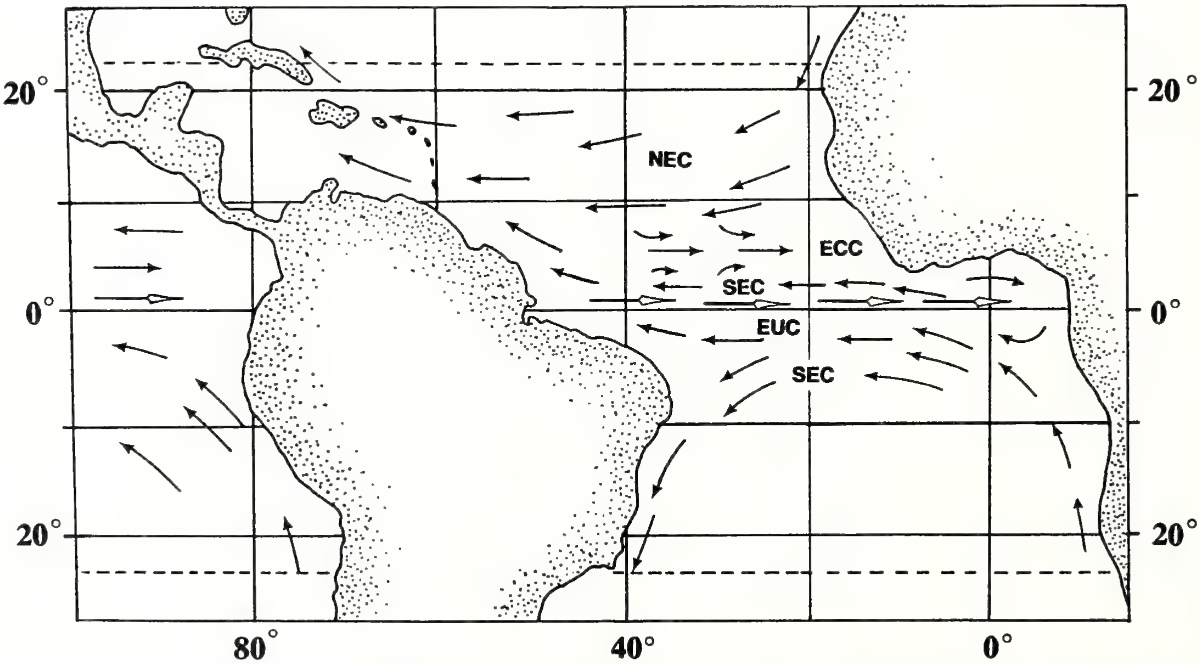

Fig. 1. Schematic illustration of major ocean currents of the tropical Atlantic Ocean. ECC, seasonally occurring Equatorial Countercurrent flowing from the western to the eastern equatorial Atlantic (see Fig. 3); EUC (large open arrows), Equatorial Undercurrent flowing from Brazil to West Africa at a depth below 50 m (see Fig. 2); NEC, North Equatorial Current flowing from northwestern West Africa to the Caribbean; SEC, South Equatorial Current flowing from West Africa to Brazil.

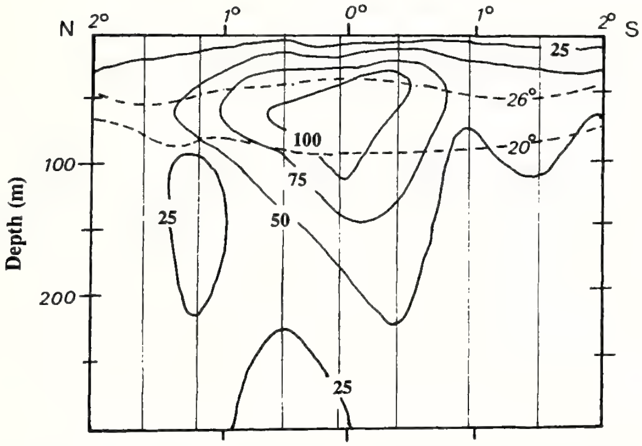

Fig. 2. North-south section across the Equator at 13°30, W illustrating the extent of the Equatorial Undercurrent. Continuous, unbroken isopleths denote current shear in cm/sec and illustrate relative differences in current velocity at various depths. Direction of undercurrent is toward the east (into the Fig.). Vertical lines show position of stations. Dashed lines indicate 26° and 20° C isotherms. (Based on Metcalf *et al.*, 1962:2503, fig. 6).

Consider now the distribution of teleplanic or "long-distance" veliger larvae of sublittoral species in relation to this tropical North Atlantic circulation. Among the most common molluscan larvae that have been encountered are those of prosobranch gastropods. At least 20 families are represented in samples within the upper 100 m. Two especially prominent are the Architectonicidae and the Ranellidae (=Cymatiidae). For example, among the Architectonicidae larvae of approximately 30 recognizable species have been encountered in the tropical and warm temperate North Atlantic Ocean. Study of the adult forms has shown that many Architectonicidae have very wide geographic distributions (Merrill, 1970; García-Talavera, 1982; Bieler, 1993); indeed Bieler *et al.* (1986:286) ventured that "most species are ... amphi-Atlantic." However, only six species of architectonicid larvae have actually been described and related to their adult forms by a comparison of their larval shell to the protoconch of identified post-larvae; two of these are Atlantic species, viz. *Philippia krebsii* (Mörch, 1875) and *Architectonica nobilis* Röding, 1798. Both are amphi-Atlantic in their geographic distribution (Scheltema, 1971b; Laursen, 1981). Thirty-four species of Ranellidae are known from the tropical Atlantic Ocean and among these over half have an amphi-Atlantic distribution (García-Talavera, 1987). Larvae of 12 Atlantic species have been described (Scheltema, 1971b; Laursen, 1981). The distributions of veliger larvae belonging to the Architectonicidae and Ranellidae obtained from plankton tows taken in the tropical Atlantic are shown in Fig. 4.

Among bivalve mollusks, the veliger larvae of the members of Pinnidae are among the largest known, some attaining a length of 700 µm before metamorphosis (Yoshida, 1956; Ota, 1961; Booth, 1979) and are readily recognized by their characteristic triangular-shaped valves. Eight species assigned to two genera, viz. *Pinna* and *Atrina*, are known from tropical and temperate Atlantic waters, and their geographic distributions were briefly described by Scheltema and Scheltema (1984). Two tropical species belonging to the genus *Pinna* are amphi-Atlantic in distribution; in contrast, all species of the genus *Atrina* are broadly distributed either along the coastlines of South America or West Africa, but none occur on both sides of the tropical Atlantic Ocean.

Veligers of the wood-boring bivalve family Teredinidae also occur in epipelagic waters of the tropical and warm temperate Atlantic Ocean (Scheltema, 1971c). Identification is possible from the configuration of the hinge teeth and shape of the valves, *i.e.* greater dorsoventrally than anteroposteriorly. Other bivalve veligers known from the Atlantic epipelagic zone include the Erycinidae, Limidae, Lucinidae, Mytilidae, Ostreidae, Pholadidae, and

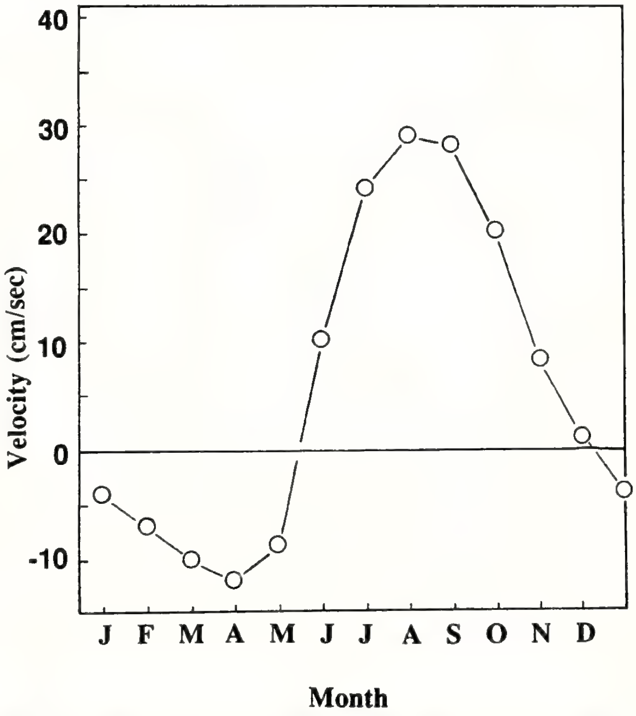

Fig. 3. Seasonal variation in mean monthly velocity of the Equatorial Countercurrent determined from ship's drift in the region bounded by 5° and 8° N latitude and 25° and 30° W longitude. Positive values indicate eastward velocity in cm/sec; negative values indicate westward flow. The countercurrent is at its maximum between June and November when its velocity ranges between 10 and 30 cm/sec. Evidence from moored current meters and from drifting buoys during 1983 showed peak velocities up to 40 cm/sec in June and July, *i.e.* earlier and with higher maximum velocities than those obtained from the set of ships. (Modified after Richardson, 1984:748, fig. 4).

Pteriidae. The distribution of bivalve veligers encountered in the tropical Atlantic Ocean is shown in Fig. 5.

The direction of mean net transport of larvae is along the axis of the major ocean currents. It cannot be assumed however that planktonic larvae will always behave as completely passive particles. The possibility remains that some larvae may control their vertical distributions and if this is so, they may utilize the Equatorial Undercurrent (Fig. 2) which moves in the opposite direction to that near the surface. There is at present, however, only little known about the behavior of teleplanic larvae (Scheltema, 1972a).

Evidence from the observed distributions of teleplanic larvae and from advection by ocean currents provides a compelling argument for long-distance larval dispersal of tropical molluscan species. Minimum and maximum average current velocities of 25-100 cm/sec can result in passive dispersal of larvae between 22 and 90 km/day and crossing of the tropical Atlantic Ocean (ca. 5000 km) in 55-195 days or a mean of about four months.

What is the likelihood that a larva will be transported passively across the Atlantic Basin? The drift coefficient for the tropical and warm temperate Atlantic Ocean (*i.e.* the likelihood that a specific larva will be successfully dispersed across the Atlantic Basin) falls between 0.01 and 0.001. These values were derived from drift bottle data (Scheltema, 1971b). Although the odds seem very small, they must be related to fecundity, which in most gastropods with planktonic development is very high and, between 10^4-10^6 eggs/female/yr. Among bivalves, this value can be even higher, > 10^7 eggs/female/yr. Although the likelihood that any particular larva will be transported across the tropical Atlantic Ocean is very small indeed, there is a reasonable chance that at least some will succeed. For example, for a species that produces 0.5 million eggs/female/yr, at a drift coefficient of 0.01, between 5 and 50 larvae/female/yr will be successful, even when allowing 99% mortality from predation (Scheltema, 1971b). Plankton samples confirm that larvae actually are advected over great distances by ocean currents (Figs. 4 and 5) and laboratory observations show that teleplanic larvae taken from the plankton in fact can delay settlement and metamorphosis for periods up to five months after collection (Scheltema, 1971b).

RAFTING

An alternative to passive dispersal by means of planktonic larvae is the transport of juvenile and adult organisms by rafting on floating objects. Drifting materials that serve as rafts include plant remains such as logs, parts of fruits [*e.g.* coconut husks, seed pods and pits (Guppy, 1917; Gunn, 1968), mangrove leaves (Wehrtmann and Ditell, 1990)] or drifting algae (Vallentin, 1895; Arnaud *et al.*, 1976; Highsmith, 1985). Algae could be less effective

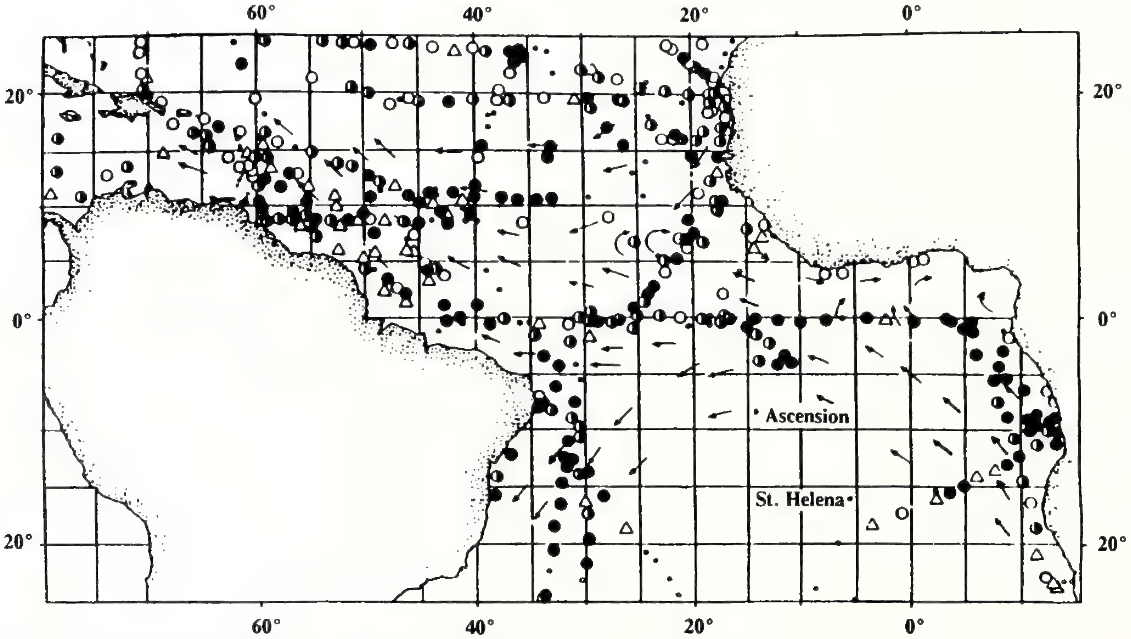

Fig. 4. Distribution of sampling locations where gastropod veliger larvae were encountered. Large filled circles, locations where larvae of the family Architectonicidae were found. Large open circles, locations where larvae of Ranellidae were encountered. Large divided circles, locations where both Architectonicidae and Ranellidae were found in the same sample. Triangles, locations where veliger larvae of 18 other gastropod families have been taken in plankton nets including Naticidae, Cypraeidae, Thaididae, Triphoridae, Coralliophilidae, Bursidae, and Tonnidae. Small open circles, locations where gastropod veligers were absent. (Redrawn after Scheltema, 1986:300, fig. 4.)

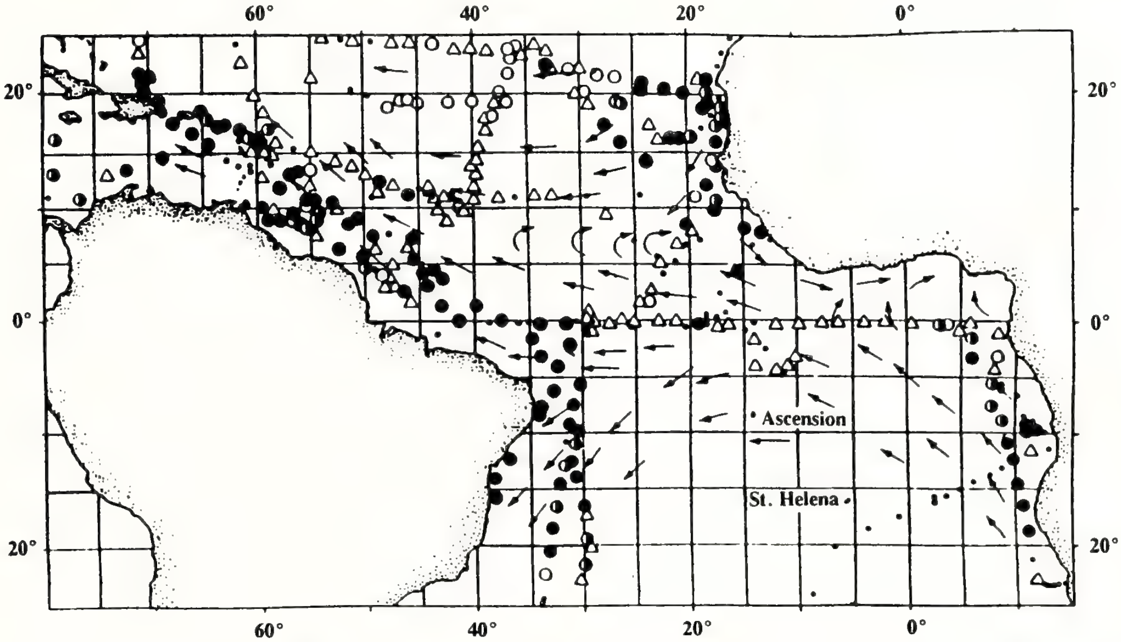

Fig. 5. Distribution of sampling locations where the bivalve veliger larvae were encountered. Large filled circles, locations where larvae of the family Pinnidae were encountered. Large open circles, locations where Teredinidae larvae were found. Large divided circles, locations where both pinnid and terridinid larvae co-occurred. Triangles, locations where larvae of other bivalve families occurred. Small open circles, sampling locations lacking bivalve larvae.

in tropical waters than at high latitudes where gastropods and bivalves can be transported in the holdfasts of enormous kelps. Carquist (1974) gave a useful summary of plants which potentially serve as rafts. Bivalves that are cemented to hard surfaces (*e.g.* oysters; Stenzel, 1971), that are attached by a byssus (*e.g.* mussels, Pinnidae), or indeed most newly settled bivalve species, can be rafted on almost any floating object. The Teredinidae, or shipworms, and other wood-boring mollusks are readily dispersed on floating timber (Turner, 1966). *Lyrodus pedicellatus* (Quatrefages, 1849), which has a planktonic larval life of about one day, has nonetheless a circumtemperate and tropical distribution. It has been suggested by Marche-Marchad (1968) that the wide geographic distributions of large volutid gastropods of the genera *Cymba* (= *Cymbium*) and *Adelomelon* which lack planktonic larval stages, can be explained by the dispersal of their egg capsules attached to drifting objects. Another form of rafting reported by Frazier *et al.* (1985) is the transport of bivalves and gastropods on the carapaces of sea turtles.

Pumice that originates from volcanic eruptions can serve as floats for a variety of invertebrate organisms (Scheltema, 1977). Floating pieces varying in size from a few millimeters to two meters in diameter were reported by Jokiel (1989), and Fushimi *et al.* (1991) found concentrations up to 500 per 1850 m^2 in the Kiroshio, North Equatorial, and Subtropical Counter Currents. Through knowledge of its relative composition, (viz. Na_2O and Kr_2O; FeO, TiO_2 and MgO; or ZnO, CuO and SrO), it is possible to infer the origins of drifting pumice by comparison with material arising from known volcanic disturbances. Jokiel (1984) made observations on reproductively mature colonies of the coral *Poecillopora* which he judged to be two to three years of age and also the calcareous encrusting remains of oysters, serpulid worms, and calcareous algae attached to drifting pumice (Jokiel 1989, 1990a).

From all of this anecdotal evidence, it seems that rafting must play a roll in the passive dispersal of at least some molluscan species, but such transport necessarily must be restricted to forms that spend most of their adult life on hard substrata. It is highly unlikely that infaunal "soft-bottom" molluscan species will ever be rafted over long distances. This is because of their inability to survive for long periods outside their normal habitat and the improbability that they can remain affixed to drifting objects for significant periods of time. Unlike planktonic larvae which may be dispersed by sub-surface currents (*e.g.* the Equatorial Undercurrent), rafting is restricted entirely to the surface. It seems probable that rafting plays only a secondary role in the dispersal of mollusks.

HUMAN ACTIVITIES

Finally, there is the possibility of dispersal of molluscan species by the activities of humans. Both attachment of mollusks to the hulls of ships and the practices used in shellfish culture have led to the dispersal of numerous gastropod and bivalve species. Recently, ballast water of ships has also been implicated in the transport of planktonic larvae over great distances. Carleton (1985) and Williams *et al.* (1988) have reviewed and given evidence for the importance of human intervention to the geographic distribution of marine invertebrate species. However, such introductions of species are probably only of marginal importance in the historical biogeography of the Caribbean as they include only a very restricted period of time (ca. 500 yrs).

OBJECTIONS TO THE HYPOTHESIS OF PASSIVE LONG-DISTANCE DISPERSAL

Four major criticisms have been raised against passive dispersal of planktonic larvae as a significant factor in determining the patterns of geographic distribution among benthic species. The first of these was most recently expressed by Jokiel (1990b:60) who maintained that "larvae generally have a fixed life span" and "the majority of invertebrates ... have larval competence periods of only a few weeks." Jokiel concluded that "even the most rapid ocean currents can transport drifting objects only a few hundred km during the life span of a typical larva." This view has its origin in a paper by Thorson (1961:472) who concluded that "eighty percent of all bottom invertebrates with pelagic larvae have a planktonic life of less than six weeks ... [and therefore] even if ... larvae are transported by especially rapid currents, they never seem to have even the slightest chance to cross the larger ocean basins." Thorson (1961) believed that only 5.5% of invertebrates had a potential planktonic life exceeding twelve weeks. However, this conclusion was based upon cold-temperate, North Sea and Baltic Sea species, and Thorson himself (1961:473) allowed that tropical species can differ from such cold-temperate forms. Thorson's data on mollusks were quite limited (Thorson, 1961:460, fig. 1). Only 18 species of prosobranch gastropods were listed, and among these none had a development exceeding nine weeks (most less than five weeks). Now 30 years later, at least 20 families of gastropods are known to have long-distance larvae; indeed within the family Architectonicidae alone, more than 30 species of teleplanic larvae have been collected in the open waters of the North and South Atlantic Oceans. Thorson (1961:466) was actually aware of at least six families of "pronounced long-distance larvae among prosobranchs" and guessed that these "might last for six months," but somehow he did not include these in his tabulations.

Subsequent observations made in the laboratory have shown that at least some tropical gastropod veligers taken far out at sea and probably already several months old when captured can delay settlement for an additional period exceeding four months duration (Scheltema, 1971b).

Bivalves also were considered by Thorson. Data for 37 species led him to conclude that most bivalves have planktonic larvae for less than five weeks. However, this estimate, as that for gastropods, was based upon Baltic Sea and North Sea species and ought not to be extrapolated to tropical forms. Bivalve veligers belonging to sublittoral species and taken in the Gulf Stream, Sargasso Sea, North and South Equatorial Currents, and the Canary, Brazil, and Antilles Currents, suggest from their position at the time of capture that they also must have been adrift very much longer than the five weeks inferred by Thorson.

Contrary to Jokiel's (1990b:60) assertion, most invertebrate larvae do not "have a fixed life span." In fact, the duration of planktonic development is usually very flexible. The length of the "precompetent" stage, which is the time of larval growth and development, is thought to be determined largely by seawater temperature and by the amount and "quality" of available food, *i.e.* by both the species and "condition" as well as by the number of such food organisms (*e.g.* for bivalves see Davis and Guillard, 1958; Bayne, 1965; Loosanoff *et al.*, 1951; Stickney, 1964; Pechenik *et al.*, 1990; Sprung, 1984; for gastropods see Pilkington and Fretter, 1970; Scheltema, 1967; Pechenik and Fisher, 1979; Lima and Pechenik, 1985). When the "competence" to settle has been achieved, often there may be, in the absence of an appropriate cue, a further delay in settlement and metamorphosis. Such a delay was demonstrated for prosobranch gastropods in *Nassarius obsoletus* (Say, 1822) by Scheltema (1956, 1961) and in *Phestilla sibogae* Bergh, 1905, by Hadfield and Karlson (1969); delay in metamorphosis has also been established for bivalves, viz. *Ostrea edulis* Linné, 1758, by Cole and Knight-Jones (1949), and Knight-Jones (1951), and for *Crassostrea virginica* (Gmelin, 1791) by Crisp (1967). The generality of such settlement responses has been amply confirmed experimentally for numerous other molluscan species. A particularly striking example of the prolongation of planktonic larval life in the absence of an appropriate cue is that of the gastropod *Aplysia juliana* (Quoy and Gaimard, 1832) which in the laboratory becomes competent to settle after only 30 days but in the absence of a cue (in this instance a green alga), can delay settlement for more than 200 days (Kempf, 1981)! It should be obvious that the length of the delay in settlement and metamorphosis could vary widely if a cue is not encountered although there is some evidence that with increasing lengths of time in the plankton the larvae of some invertebrates may become less discriminating and respond to alternative and presumably less favorable cues.

The statement by Jokiel (1990b:66) that "even the most rapid currents can transport objects only few hundred kilometers during the life span of a typical larva" ignores a large body of existing evidence. This question was addressed almost 30 years ago (Scheltema, 1966:87, table 1) when it was demonstrated that the surface current velocity was well within the time required for the larva of the gastropod *Cymatium parthenopeum* (von Salis, 1793) to cross the North Atlantic to the Azores. The current velocities in the North and South Equatorial Currents are quite sufficient to transport larvae from West Africa to South America in four to six months; likewise both the Equatorial Undercurrent and Equatorial Countercurrent (during summer months) are sufficient to passively disperse larvae in the opposite direction from South America to West Africa.

A second criticism has been expressed by Mitton *et al.* (1989:360) who noted that it is not known "whether a significant proportion of larvae found in the middle of the ocean are [still] capable of metamorphosis and survival," and hence whether teleplanic larvae can contribute to downstream populations. Laboratory experiments have shown that at least some molluscan larvae taken alive from the open waters of the Atlantic Ocean retain the capacity to metamorphose. For example, veligers of gastropod species in the families Architectonicidae, Ranellidae, Coralliophilidae, Cypraeidae, Naticidae, Neritidae, Ovulidae, Strombidae, Tonnidae, Triphoridae, among others, as well as in the bivalve families Pinnidae, Erycinidae, Limidae, Mytilidae, Ostreidae, Pholadidae, Pteriidae, and Thyasiridae have been shown to metamorphose in the laboratory when removed from samples obtained hundreds of kilometers out at sea (Scheltema, unpub. data). Clearly additional observations on a wider spectrum of molluscan species and families would be useful. Nevertheless, observations up to now show that in most known instances teleplanic larvae do in fact retain their ability to metamorphose.

A third objection is the claim by vicariance biogeographers that long-distance or "jump" dispersal cannot explain patterns of distribution or the relationships between widely separated faunas because such a process is random and therefore cannot account for the congruent, nonrandom geographic associations found among numerous, widely differing taxa. For example, Croizat *et al.* (1974:267) maintained that the "means of dispersal ... vary from species to species and do not explain patterns of biotic distribution." This assertion is arguably true for terrestrial forms but is irrelevant for a wide spectrum of sublittoral marine mollusks. This is because the principal means of dispersal among terrestrial species is *active migration* by adults (Scheltema, 1986, 1989a), whereas most tropical sublittoral or benthic marine molluscan species (ca. 70-80%) have planktonic larval stages which are *passively* dispersed (Thorson, 1950).

It is true that passive dispersal can result from both eddy diffusion and advection. However, eddy diffusion is the random dispersal that results from turbulent flow. Its horizontal component along a two-dimensional surface can be measured by the mean change in distance between freely drifting objects. Dye experiments in a number of locations in the North Atlantic Ocean have shown that over the period of one month, eddy diffusion alone accounted on average for maximum dispersal to within a radius of about 100 km (Okubo, 1971). But the larva dispersed passively by eddy diffusion theoretically can be found anywhere within such a 100 km radius, *i.e.* both the direction and rate of dispersal will be unpredictable. Thus while 100 km defines the upper limit of dispersal, most larvae will be transported over much shorter distances (see Okubo, 1994, for a more comprehensive and mathematical treatment of eddy diffusion and its role in larval dispersal).

Advection, in contrast, is the non-random, directed, horizontal transport within a defined current regime and is the horizontal displacement with respect to a set of fixed coordinates. The direction of the mean net transport will be along the axis of the current. The rate of flow of the major tropical Atlantic circulation, as already related above, ranges from about 25 to more than 100 cm/sec; by comparison the maximum mean rate of horizontal dispersal from eddy diffusion will scarcely ever exceed 4 cm/sec and its net direction will be random. Because eddy diffusion and advection occur simultaneously, larvae will be both randomly dispersed with respect to one another while at the same time advected along the axis of the current. At a biogeographically relevant scale, it is reasonable to conclude that dispersal results largely from advection along ocean currents; eddy diffusion probably plays only a minor role in the geographic distribution of sublittoral marine molluscan species (Scheltema, 1986:fig. 1) although possibly it has other significant consequences (Strathmann, 1974).

Planktonic larvae of widely different species can and do co-occur within the same major ocean currents. The major current systems of the tropical Atlantic Ocean provide quasi-permanent or in some instances seasonably reoccurring corridors for the transport of molluscan larvae quite irrespective of their taxonomic affinity. All passively advected larvae are necessarily dispersed over similar routes and such transport can be expected, on average, to result in congruent geographic distributions among widely different molluscan taxa. A fundamental difference exists between active dispersal directly related to the behavior of an individual, as commonly encountered among terrestrial organisms, and passive dispersal which depends solely upon the direction and velocity of ocean currents.

A fourth criticism due to Turner (1966), Bhaud (1982), Jackson (1986), and most recently Jokiel (1990b), is that many benthic invertebrate species, even though they lack a long planktonic larval development nevertheless have very large geographic ranges. It already has been shown above that rafting can provide an alternative means of passive dispersal, but also that such a mode of transport necessarily is restricted to organisms that can remain attached to hard substrata over long intervals of time (*e.g.* bryozoans, hydrozoans, barnacles, teredinids, some bivalves, etc.). Excluded, as may be verified by examining floating objects, are infaunal species normally found living within benthic sediments. Further, because the proportion of tropical sublittoral species that lack planktonic larval stages is relatively small, rafting although sometimes effective is limited to only a small proportion of benthic mollusks. Another explanation for large disjunct geographic distributions of mollusks results from human activity, and also has already been considered. The role of human intervention evidently is increasing and is sometimes of great economic importance. Nonetheless, it must be relatively minor when considering the biogeography of the entire Caribbean molluscan fauna.

EVIDENCE FOR ECOLOGICAL FACTORS RESTRICTING THE DISTRIBUTION OF TROPICAL WESTERN ATLANTIC MOLLUSKS

Bhaud (1993) argued and concluded correctly that the capacity for dispersal is not the sole condition which contributes to the geographic distribution of benthic species. Despite the readily demonstrable, widespread passive dispersal of larvae, and also in some instances the rafting of molluscan species over very long distances, there are also ecological constraints which place restrictions upon where and when newly settled colonizers can survive and reproduce. It is obvious that species well-adapted for the tropics cannot exist at high latitudes; likewise most polar and cold-temperate species will not be able to survive in the tropics.

Indeed, temperature sometimes plays a significant role in limiting the latitudinal distribution of benthic species. Such a relationship was already well-established more than a century ago. Darwin (1859:311) remarked that "Change of climate must have had a powerful influence on migration: a region when its climate was different may have been a high road for migration, but now impassible." Bousfield and Thomas (1975:figs. 1-9) have considered such an instance of climatic change on the post glacial distribution of littoral marine invertebrates along the Canadian Atlantic Region over the past 15,000 years. Hutchins (1947) has usefully discussed the contemporary role of temperature in a monograph entitled "The bases for temperature zonation in geographical distribution."

As an illustration, consider the blue mussel *Mytilus edulis* Linné, 1758, a boreal species which in the western North Atlantic Ocean is found southward along the North American coast as far as Beaufort, North Carolina (ca. 34°30'N) where it occurs only irregularly and then only during the winter and early spring. Here adult size or reproductive maturity are never achieved. In contrast, proceeding from Cape Hatteras northward (> 35° N) *M. edulis* can be found in any suitable habitat throughout the year. Beaufort populations clearly must represent the extreme southern limit at which larvae will survive and to which they are successfully dispersed, but newly attached juveniles never survive summer seawater temperatures which range between 25° and 30° C. Although expatriate or "pseudo-populations" can be established early during most years, no permanent or reproducing populations have ever been established (Wells and Gray, 1960).

The opposite situation has been demonstrated for the tropical amphi-Atlantic gastropod, *Cymatium parthenopeum*. Larvae are known to occur throughout the Gulf Stream and North Atlantic Drift (Scheltema 1966, 1971a, b), and adult specimens of this tropical form have been found alive by dingle fishermen off the western Irish coast (O'Riordan, 1977). It is inferred that the origin of such individuals is most likely to have been the Caribbean and that their veligers have been passively transported along the Gulf Stream and North Atlantic Drift. Because there is at least a 10°C difference in summer surface temperature between the Caribbean and the western coast of Ireland, it seems improbable that *C. parthenopeum* will ever reproduce off the western Irish coast and that therefore this population probably is an expatriate, non-reproducing one.

On a smaller scale, other characteristics of the environment will limit spatial distribution or sometimes the geographic range of species. In most instances, species adapted to rocky intertidal shores cannot exist upon intertidal marshes [although exceptions exist, *e.g. Littorina littorea* (Linné, 1758)] nor can infaunal species of intertidal flats exist in the surf of sandy coastal beaches. Physical heterogeneity as well as various biological interactions at differing spatial scales (from meters to kilometers) can result in disjunct distribution *within* a species' geographic range. Although ecological factors can set distinct limits for the distribution of species, *e.g.* temperature may determine the northward and southward latitudinal range, much of the small scale physical and biological heterogeneity of the environment can play only a secondary or minor role in determining species distribution on a biogeographically relevant scale. Because this review deals primarily with passive dispersal, a detailed discussion of the ecological effects on biogeographic distribution is not undertaken here.

GEOTECTONICS, SEA-FLOOR SPREADING, AND GEOGRAPHIC DISTRIBUTION OF TROPICAL MOLLUSCAN FAUNAS

Any consideration of the contemporary distribution of marine sublittoral molluscan faunas must also account for tectonic events in the geologic past and how such activity could have affected the extent of passive dispersal (Darwin, 1859:311). Significant among these are such vicariant events as: (1) the opening and closing of seaways or corridors which may either facilitate or, alternatively, completely prevent any passive dispersal (Hallam, 1973), and (2) continental drift and sea-floor spreading leading to the initial formation and subsequent enlargement of ocean basins (Berggren and Hollister, 1974).

TETHYS, THE CENTRAL AMERICAN CORRIDOR, AND THE PASSIVE DISPERSAL OF TROPICAL MOLLUSKS

During the Middle Cretaceous and Early Tertiary, the Tethys Sea provided a route through which species could be passively dispersed between the tropical waters of the Indo-Pacific and eastern proto-Atlantic Oceans (Fig. 6). Similarly the corridor between North and South America allowed passive dispersal between the tropical western Atlantic and eastern Pacific Oceans. Thus during the Middle Cretaceous, a circumglobal seaway existed, providing continuity among tropical oceans throughout the world.

Luyendyk *et al.* (1972) inferred from tank studies using a planetary vorticity model that during the Middle Cretaceous (ca. 100 million years ago) a circumglobal circulation existed from east to west with an average velocity of 2-4 knots (*i.e.* ca. 100-200 cm/sec). More recently, Barron and Peterson (1989:685) devised a three-dimensional numerical model of Middle Cretaceous circulation which also included sea-level and climatic changes and (in contrast to Luyendyk *et al.*, 1972) concluded that although circulation in the tropical Pacific Ocean did indeed appear to flow from east to west, that of the Tethys Sea showed "a clockwise flow, which produced a general eastwardly flow along [its] ... northern margin. The clockwise, gyre-type circulations that develop between North and South America and between Eurasia and Africa yield components of [both] westward [and] ... eastward flow." Van Andel (1979:18)

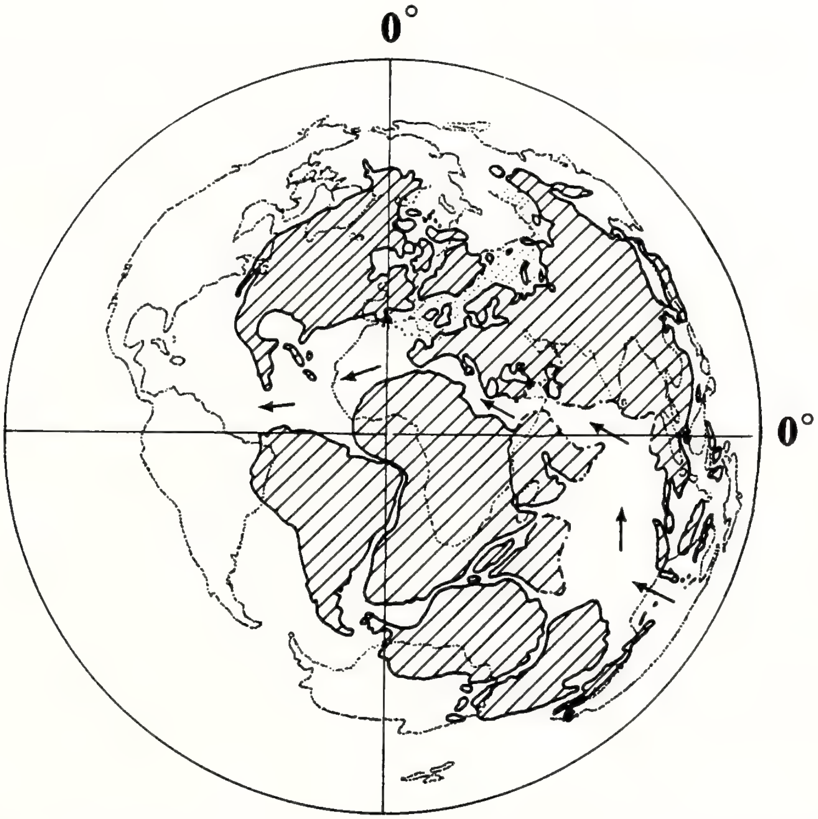

Fig. 6. Disposition of continents during the Middle Cretaceous (slashed areas) and their present positions (stippled outlines) showing the displacement of continents over the past 100 million years. Arrows indicate the circumtropical connections by way of the Tethys Sea (between Asia and Africa) and through the corridor between North and South America. During the next 35 million years, the North Atlantic enlarged and the South Atlantic began to open. (Modified from Briden *et al.*, 1974:figs. 1, 5; see also Fig. 7).

believed that "for some time during the Miocene, Pacific water may have flowed eastward into the Caribbean through the isthmus area."

Observations on contemporary long-distance transport of planktonic larvae together with a knowledge of major seaways, corridors, and ocean basins during the Tertiary allows inferences to be made about passive dispersal of molluscan veligers during the geologic past. However, to deal with specific instances, one must know something about the life history of fossil species (Jablonski and Lutz, 1983). Such information can be obtained in well-preserved fossil gastropods from the protoconch, *i.e.* the larval shell at the apex of the adult or juvenile shell (Thorson, 1950; Shuto, 1974; Jung, 1975; Scheltema, 1978) and from the prodissoconch or larval shell at the umbo of postlarval bivalves (Ockelmann, 1965; Lutz and Jablonski, 1978). Inspection of the protoconch or prodissoconch makes it possible not only to determine the mode of development, *i.e.* whether or not a species had planktonic development, but sometimes also to roughly approximate the length of time adrift, and hence to discriminate between species with actaeplanic larvae that have relatively short planktonic lives of only a few weeks (Scheltema, 1989b:186) and those with teleplanic veligers that may remain planktonic for many months. For example, comparison of the protoconchs of fossil specimens of *Architectonica nobilis* from the Miocene, Pliocene, and Pleistocene (Woodring, 1959:165) with those of contemporary specimens of the same species shows that the mode of development remained unchanged and allows the inference that long-distance dispersal of *A. nobilis* larvae must have been much the same during the Miocene as it is today (Scheltema, 1979). Similar inferences can be made with extinct congeners, especially when the life histories of present-day species are known.

When the life histories of Tertiary mollusks are considered in relation to the known tectonic events since the late Oligocene (a period of about 40 million years), it seems highly probable that species with planktonic larvae would have had the opportunity for passive two-way dispersal between both the tropical western Indo-Pacific and eastern Atlantic Oceans (Kauffman, 1975) through the Tethys seaway and between the Caribbean and eastern tropical Pacific Ocean by way of the Central American Corridor (Woodring, 1966). Hence, tropical Tertiary species with teleplanic larvae, such as Architectonicidae and Ranellidae, could have been dispersed during the early Tertiary by the ocean circulation that existed at that time. However, the Tethys was a shallow epeiric sea, so it is likely that even a species with a relatively short planktonic larval development could have passed through to the eastern proto-Atlantic by stepwise dispersal over many generations (Scheltema, 1989a).

Kauffman (1975:183, Fig. 2) made substantially similar arguments for the dispersal of bivalve larvae and wrote, "The larvae of Cretaceous bivalves should have been able to disperse through the Euramerican Region and across the Atlantic extension of the Tethys in short 'geologically instantaneous' periods of time."

The open circumglobal seaway first became obstructed in the southeast Asian region by the Early Oligocene (ca. 35 million years ago) and in the Mediterranean and Near East in the Late Oligocene or Early Miocene. The corridor between North and South America closed much later, in the Early Pliocene (Van Andel, 1979:17), and resulted from the eastward movement of the Caribbean plate (Williams, 1986:11, fig. 6). As a result of such tectonic activity, three major marine tropical biogeographical regions appear to have arisen. These were: (a) the Atlantic (including the Mediterranean); (b) the Indo-West Pacific including the Indian Ocean, the western Pacific, and the Central Pacific Islands; and (c) the East Pacific, including the tropical western coastline of Central and South America. Bieler recognized these three regions in a study of the Architectonicidae (Bieler *et al.*, 1986; Bieler, 1993) and proposed that a major radiation leading to Recent species took place before the separation of the major oceans in the Miocene and Pliocene. He concluded, "The differences between the three modern architectonicid faunas can be explained by Post-Pliocene extinction of different parts of the Neogene stock in the Eastern Pacific and in the Atlantic" (Bieler *et al.*, 1986:236).

Among the Ranellidae, the relationship between the Indo-Pacific, Atlantic, and East Pacific is not as easily demonstrated because of taxonomic difficulties within the family (Beu and Kay, 1988), but it is apparent nonetheless that much of the biogeography of species in this family is explicable only by reference to long-distance dispersal of teleplanic larvae and to the tectonic events that occurred during the Middle and Late Tertiary.

SEA FLOOR SPREADING, PALEOCIRCULATION, AND THE PASSIVE DISPERSAL OF TROPICAL MOLLUSKS IN THE ATLANTIC OCEAN

The paleogeography and paleocirculation of the Alantic Ocean, from its origin in the Triassic ca. 200 million years ago until the present, were summarized by Berggren and Hollister (1974). Sea-floor spreading throughout the Tertiary resulted in the ever-increasing size of the Atlantic Basin and a concomitant increase in the distance between the tropical eastern Atlantic Ocean and the Caribbean Sea (Fallow, 1979; Fallow and Dromgoole, 1980). As the Atlantic Ocean increased in size (Fig. 7), the possibility of passive trans-Atlantic dispersal on ocean currents became increasingly more difficult for those species whose larvae had only relatively short planktonic development or whose capacity to delay settlement was limited to only a few weeks. Such time constraints did not apply to rafted organisms so long as they were able to survive at sea, but rafting as already noted is restricted mostly to epibenthic species that live their adult life permanently attached to hard substrata.

Differences in the amount of time required for dispersal between the tropical eastern and western Atlantic at various epochs throughout the Cenozoic can be estimated from the mean width of the Atlantic Basin and from the inferred surface currents based on experimental tank studies (Luyendyk *et al.*, 1972). Values in Table 1 show that during the Paleogene, passive dispersal of planktonic larvae would have required two to five weeks, well within the capacity of most contemporary molluscan species. However, after the Oligocene and throughout the Neogene the time needed for passive transport across the Atlantic Ocean progressively increased owing to the greater distance between continents (Berggren and Hollister, 1974) and also to a decrease in current velocity (Luyendyk *et al.*, 1972), so that in the Holocene two to six months are required. Indeed, the Cenozoic fossil record appears to show an inverse relationship in the similarity coefficient of invertebrate genera occurring on either side of the Atlantic Ocean and the width of the Atlantic Basin (Fallow, 1979; Fallow and Dromgoole, 1980). An increase in the size of the Atlantic Basin seems to have acted as a "filter" for exchange between the fauna of the eastern and western tropical Atlantic. Only species having larvae with a long planktonic development and capacity to delay settlement are today able to successfully make a trans-Atlantic crossing. Yet, a substantial number of species appear to have such a capacity (García-Talavera, 1982).

Obviously, successful trans-Atlantic crossing of larvae must have been much more likely in the Early Tertiary than it is today; nonetheless the veligers of many contemporary molluscan species continue to have the potential to cross the "mid-Atlantic barrier."

CONSIDERATIONS ARISING FROM GEOGRAPHIC DISTRIBUTION

The account given in the previous pages shows that the principal source of the Caribbean molluscan fauna most likely was the eastern tropical Atlantic, which in turn was

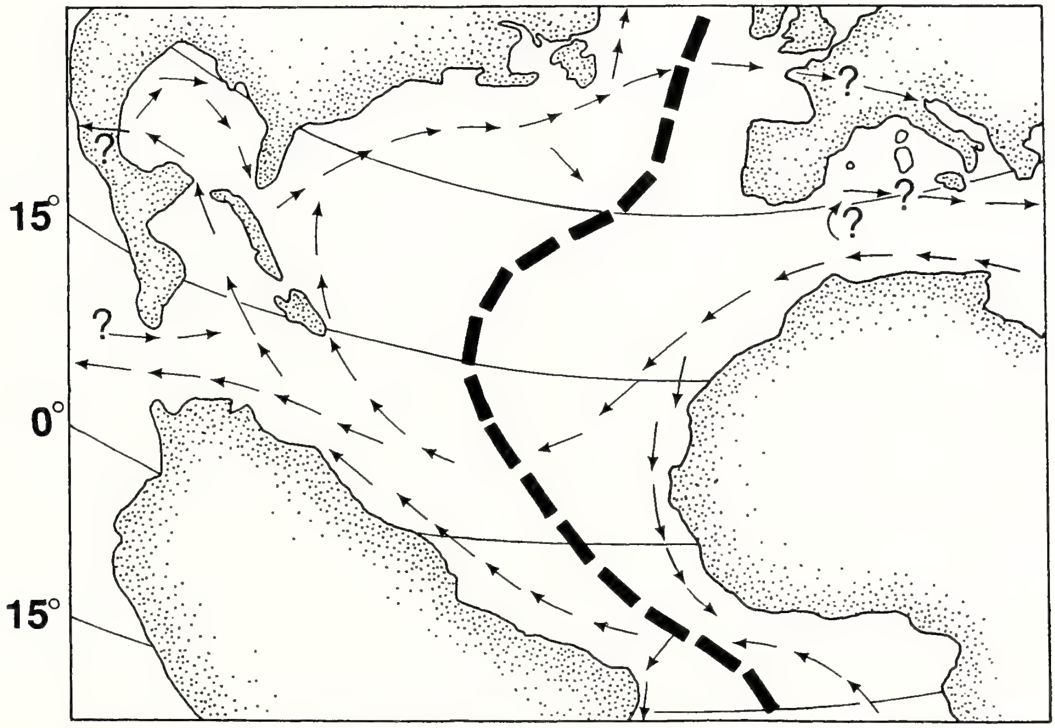

Fig. 7. Atlantic paleogeography and inferred paleocirculation at the end of the Cretaceous, 65 million years ago. Small arrows show surface circulation. Question marks show regions where some uncertainty still exists regarding the direction of currents. Dark dashed line indicates approximate position of the Mid-Atlantic Ridge from which sea-floor spreading is initiated and which has resulted in the ever-increasing size of the Atlantic Basin. Shallow sills occurred at the mouth of the Tethys Sea ("Mediterranean") and the corridor between North and South America. (Modified after Berggren and Hollister, 1974, with additional data from a three-dimensional numerical model by Barron and Peterson, 1989).

derived largely during the Late Cretaceous and Early Tertiary by way of the Tethys Sea. The question arises, what can a comparison of the contemporary faunas indicate about such relationships? What does geographic distribution reveal about the possible role of passive dispersal?

EVIDENCE FOR THE DISTRIBUTION OF GENERA

Among the gastropod genera occurring on the West African coast, approximately two-thirds are found also in the western tropical Atlantic. Specifically, of the 287 contemporary gastropod genera recorded by Nicklés (1950), Gofas *et al.* (1989), and Nordsieck and García-Talavera (1979) along the west coast of Africa and closely associated islands, 198 or about 65% occur also in the Caribbean Sea. Similarly among the 94 West African bivalve genera, 70 or about 75% are also found in the tropical and warm-temperate western Atlantic. Furthermore, a comparison between the tropical eastern Atlantic and eastern Pacific shows that 140 or 49% of West African gastropod genera also occur in the tropical eastern Pacific. The above values have been derived by the comparison of West African molluscan genera from sources cited above with those recorded by Abbott (1974) in the Caribbean and by Keen (1971) in the eastern Pacific.

Whether or not these values are truly representative remains problematic; they however can be of only limited value for making inferences about the relationship of the Caribbean and eastern Pacific fauna to that of the eastern tropical Atlantic Ocean inasmuch as no fossil genera have been included. The values perhaps do allow the tentative conclusion that the Caribbean fauna is represented (along with some endemic taxa) by an attenuated representation of tropical eastern Atlantic genera, and that the eastern tropical Pacific fauna is derived largely from the tropical Atlantic. This is so because the wide expanse of the Pacific Ocean acts as a substantial barrier to dispersal and as Darwin (1859) observed is an almost "impossible barrier" for the migration of coastal marine animals from the western to eastern tropical Pacific (but see Emerson, 1991; Scheltema, 1988).

EVIDENCE FROM SPECIES DISTRIBUTIONS

Recognition of the differences and similarities of species composition between the eastern and western tropical Atlantic faunas may lead to further insights about processes that have led to the present Caribbean fauna. Such comparisons between faunas are most easily accomplished by use of a database such as that devised by Rosenberg (1993) for the Caribbean. It is however doubtful that a meaningful or reasonably complete compilation of West African marine molluscan species could be made from the existing literature.

Table 1. Time required for passively transported larvae to cross the tropical Atlantic Ocean during the Late Cretaceous and Cenozoic (after Scheltema, 1986).

Average width of ocean (km)*	Geological epoch or period	Time required to transverse Atlantic (wk)**
2,248	Upper Cretaceous to Tertiary	1.8-3.6
2,507	Paleogene to Eocene	2.1-4.2
3,215	Eocene to Oligocene	2.5-5.2
3,852	Early Miocene	6.4-19.1
4,194	Late Miocene	8.3-25.0
4,752	Holocene	9.2-28.3

*Values taken from Fallow and Dromgoole (1980); mean width of the present tropical Atlantic Ocean taken from contemporary charts.

**Computed from current velocities derived experimentally by Luyendyk *et al.* (1972). Tank model studies suggest velocities of 3.7-7.4 wk during the Early Tertiary. At the close of the Tethys Sea (Oligocene), the current velocity was reduced to 1-3 km/hr and these values were used in computations made between Early Miocene and Holocene.

Notwithstanding, some useful information on amphi-Atlantic molluscan distribution does exist, which although incomplete allows at least some comparisons. Templado *et al.* (1990) have complied an annotated list of 182 species of opisthobranchs among which 22.5% have amphi-Atlantic distributions. Although some of these species may have rafted on algae, it was considered that most of the distributions could be accounted for by larval dispersal. Edmunds (1977) determined that among 37 species of opisthobranchs from Ghana, 43% also occurred in the Caribbean or Brazil, and Marcus and Marcus (1966) estimated that 29% of the West African opisthobranchs from the Gulf of Guinea were amphi-Atlantic. Nordsieck and García-Talavara (1979) listed 50 species (8.7%) of prosobranch gastropods from Macronesia (mostly from the Canary Islands) that also occur in the Caribbean Sea. García-Talavera (1982) enumerated 102 amphi-Atlantic species of prosobranch gastropods from the Canary Islands. In a study of the family Ranellidae from the Atlantic Ocean, García-Talavera (1987) found 17 of 36 species were known to have amphi-Atlantic distributions. Most Architectonicidae are thought to have amphi-Atlantic ranges (Bieler *et al.*, 1986). From the above data one is encouraged to believe that the Atlantic Basin is not at present a complete barrier to exchange between the tropical eastern and western Atlantic and that genetic continuity between widely separated populations of some molluscan species is possible even today. On the other hand, the closure of the corridor between North and South America (*i.e.* the Panamanian Isthmus) has served as a complete barrier to dispersal by any natural means since the Early Pliocene thus precluding any exchange for 3 million years. Creditable inferences about the role of dispersal for determining geographic distributions of molluscan species requires a knowledge of natural history and mode of reproduction but such data are at present largely wanting for most species.

EXTINCTION AND SPECIATION

Two possible reasons have been suggested for the differences encountered between the faunas on opposite shores of the tropical Atlantic Ocean. These are: (1) extinction, *i.e.* when a species becomes extinct in one of the two disjunct regions of its original range, and (2) speciation, in which the two disjunct regions wherein a species originally occurred become sufficiently isolated that gene flow is completely prevented and, owing to differential phyletic changes between the populations, allopatric speciation eventually occurs. Vermeij (1978) allowed that it is impossible from Recent fauna alone to determine whether differential extinction or speciation have occurred; it is necessary to consult the fossil record in order to address such questions. A number of authors have recently dealt with the question of extinction of Caribbean mollusks, particularly in comparison with the eastern Pacific (*e.g.* Allmon *et al.*, 1993; Jackson *et al.*, 1993). It is not within the scope of the present paper to deal with this question.

ROLE OF DISPERSAL

The question of isolation necessarily is concerned with the lack of dispersal between two widely disjunct regions within the range of a species. Whenever a widely distributed genus includes only few species, one may suspect that dispersal has played, and continues to play, a role in the distribution of such a genus. Genetic continuity is maintained between populations and consequently allopatric speciation is unlikely to occur. In contrast, a widely distributed genus with many species is likely to result when populations become isolated in a heterogenous environment thereby leading to species radiation.

There is in fact some circumstantial evidence that a relationship exists between the capacity to disperse and the amphi-Atlantic distribution of species. For example, among the 102 amphi-Atlantic species considered by García-Talavera (1982) 96% are known to have planktonic development. Scheltema (1989b) found that among 87 species of gastropods for which the mode of development was known, 22 had teleplanic larvae and among these, 19 species were known to have amphi-Atlantic distribution. Is there then any evidence that morphological differences between widely separated populations are related to the capacity of larvae to disperse? Scheltema (1972b:113) found "among five gastropod species ... a remarkable direct correspondence between the estimated frequency of larval dispersal and the degree of morphological similarity of eastern and western Atlantic populations. Adults of species estimated to have a high frequency of larval dispersal showed little or no differences between the eastern and western-Atlantic. Conversely, species that have a restricted larval dispersal ... [were] represented by different subspecies on either side of the Atlantic ... [This] suggested that the frequency of larval dispersal and the rate of gene-flow are related" in the five species examined. Since the time of these observations, it now has become possible through new techniques in molecular biology to make estimates of gene flow, yet no research seems to have revealed the relationship between any tropical amphi-Atlantic molluscan species.

COLONIZATION OF ISLANDS

The colonization of Atlantic oceanic islands provides yet other compelling evidence for the effectiveness of passive long-distance dispersal in establishing the geographic distribution of species and in affecting the composition of tropical Atlantic faunas. Indeed, island colonization seems to provide a model of how long-distance dispersal works. Ascension Island (probably of Late Pleistocene age) is located in the tropical South Atlantic (7.57° S; 14.22° W) where it arises from the Mid-Atlantic Ridge. Rosewater (1975) found that the endemism of marine mollusks was less than 8% and that the remaining 92% were continental species with about equal numbers originating from the eastern and western Atlantic. Rosewater considered that the continental species must have originally colonized the island as teleplanic larvae. Analogous situations have been described by Pawson (1978) for echinoderms and for decapod Crustacea by Manning and Chace (1990). Older oceanic islands originating from the Mid-Atlantic Ridge at some earlier geologic epoch (*e.g.* the Canary and Cape Verde Archipelagos) show much higher endemisms of marine mollusks than that found on Ascension Island owing, it must be supposed, to the longer time over which species radiation can have occurred. The Canary and Cape Verde Islands as a result of sea-floor spreading have moved eastward from their point of origin on the Mid-Atlantic Ridge, and as a result are closer to the source of passively dispersing planktonic larvae from the west coast of Africa and more remote from any western Atlantic source. Consequently these island groups naturally have a larger proportion of West African marine mollusks and a much lower percentage of South American species. In a contrasting example, Leal (1991) found in the study of four tropical oceanic islands off the coast of Brazil (viz. Atol das Roccas, Fernando do Noronha, Trinidade, and Martin Vaz) that the total number of Brazilian species decreased with increasing distance from the continent and that there occurred only a very small proportion of eastern Atlantic forms. In the case of the Canary and Cape Verde Islands, one can speculate that most of the endemics will be related to western Atlantic species owing to the ever-increasing distance from a western Atlantic source and the consequent restriction over time of genetic exchange with South American species, resulting eventually in complete isolation and allopatric speciation.

CONCLUSIONS

No single process can completely explain the contemporary composition of the Caribbean tropical fauna. It has been argued from the evidence presented here that most of the Caribbean tropical molluscan fauna had its origin by passive dispersal of planktonic larvae originating from the eastern tropical Atlantic and ultimately from the Indo-Pacific by way of the Tethys Sea. With the close of the Tethys Sea during the Oligocene and Miocene, the eastern Atlantic Ocean became isolated from the Indo-Pacific region. Likewise, the close of the North and South American Corridor during the Early Pliocene resulted in complete isolation of the Caribbean from the eastern Pacific fauna. Disappearance of these two seaways resulted in almost complete isolation between faunas of the affected regions. Indeed, natural selection or genetic drift in some instances has led to allopatric speciation and to geminate pairs or sister species (*e.g.* between the tropical eastern Pacific and western Atlantic; Vermeij, 1978). Alternatively, some species have become extinct on either one or the other side of the interposed barriers.

The initial formation of the Atlantic Ocean during the Triassic and its enlargement by sea-floor spreading throughout the Cretaceous and Tertiary resulted in the establishment of a "mid-Atlantic barrier" which increasingly over time has acted as a filter for passive dispersal. The result is a reduction in the number of species found in common between the eastern tropical Atlantic and Caribbean Sea, particularly among forms with a restricted capacity for long-distance dispersal (*i.e.* those having a relatively short planktonic larval development or an inability to prolong planktonic life) or which are not adapted for long-distance rafting. However, the biogeographic evidence suggests that within the recent geologic past (*i.e.* Pleistocene) and even into the present, long-distance larval dispersal continues to play an important role, both for the initial colonization of oceanic islands (*e.g.* Ascension Island) and for genetic exchange or "gene flow" between the eastern and western tropical Atlantic Ocean.

Biogeography is now at a turning point where new techniques, *e.g.* the measurement of enzyme variation and mitochondrial DNA polymorphism, will make it possible to address questions heretofore largely intractable. Some of these possibilities using such techniques were summarized by Ward (1989). Olson *et al.* (1991:357) wrote that "the inability to distinguish between marine invertebrate larvae of closely related taxa is a longstanding problem ... within groups such as bivalves ... The larvae of many species are so similar that they cannot be identified by morphology alone. Using the polymerase chain reaction [PCR] to amplify and sequence mitochondrial DNA, ... [it is possible] to distinguish between morphologically identical co-occurring larvae of two species .... [The] technique should prove effective for the identification of larvae even when they are far from their adult population, such as open-ocean (teleplanic) larvae."

The measurement of geographic variation by the use of morphological characters can now be augmented by new biochemical techniques, and it also could become possible to make realistic measurements of genetic exchange between disjunct, widely-distributed populations. Finally cladistics, although largely ignoring the *processes* that determine the distribution of species, can allow a better understanding of existing geographic relationships such as that between the eastern and western Atlantic by recognizing large scale patterns of distribution in relation to the evolution of molluscan species. However, better knowledge of the systematics of contemporary and fossil species will be required.

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Reproductive seasonality, periodicity, and associated behavior in a colony of *Strombus pugilis* (Mollusca: Gastropoda) in Puerto Rico

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Abstract. This work focused on defining seasonal reproductive dynamics and individual reproductive behavior for the West Indian fighting conch, *Strombus pugilis* Linné, 1758, in Puerto Rico. A colony of *S. pugilis* was followed from September 1987 to September 1989. For both years, reproductive activity began in March, when water temperature rose, and ended in November, when temperature dropped. By December, the entire colony had buried and remained so until re-emergence in February. During the reproductive season, mating and spawning activity occurred on a monthly basis with some irregularity. The monthly periodicity was significantly correlated with the lunar cycle, with peak spawning occurring in the second week following a full moon. Observations of conch held in an outdoor tank at the laboratory showed that winter burial, spring emergence, and reproductive seasonality and periodicity coincided with the same events in the field, despite a different ambient temperature regime.

The reproductive season in strombids is protracted with multiple spawnings (D'Asaro, 1965; Brownell, 1977; Kuwamura *et al.*, 1983; Weil and Laughlin, 1984). Reproductive activity decreases or ceases altogether during winter months, possibly due to the drop in water temperature (Brownell, 1977; Kuwamura *et al.*, 1983). Spawning has been observed year-round for *Strombus pugilis* Linné, 1758, in Barbados (Bradshaw-Hawkins, 1982) and *S. costatus* Gmelin, 1791, in Puerto Rico and the Turks and Caicos Islands (pers. obs.), but ceases in winter in the Yucatan (L. A. Rodríguez Gil, pers. comm.). Gametogenesis occurs year-round in *S. gigas* Linné, 1758, in Belize (Egan, 1985), although spawning has not been observed. Stoner *et al.* (1992) suggested that reproductive activity in *S. gigas* in the Bahamas is influenced by a combination of daylength and water temperature. The variability in reproductive seasonality among strombids at different locales does not allow extrapolation of such data to other areas.

Reproductive periodicity within a season has not been noted in any strombid species with the exception of *Strombus pugilis* (*fide* Percharde, 1968, 1970). Percharde (1968, 1970) casually noted cyclic burying and reproductive behavior, and suggested that lunar periodicity acted as a cue to induce spawning activity in *S. pugilis*. Reproductive periodicity was observed in a population of *S. pugilis* in Puerto Rico (Sanders, 1988), but not studied.

This study was undertaken to follow the yearly cycle of reproduction in a colony of *Strombus pugilis* to document reproductive seasonality and periodicity, if any, in Puerto Rico. Secondary objectives were to observe behavior associated with the reproductive cycle and to compare observations made in the field to those made at the laboratory.

METHODS

The colony of *Strombus pugilis* chosen for study was located one km off the town of La Parguera on the southwestern coast of Puerto Rico, at a depth of 10 m, near Corona de Piedra reef. The substratum was muddy-sand with patches of interspersed macroalgae (primarily *Halimeda, Ulva, Penicillus*, and *Caulerpa* spp.). Beginning in October 1988, bottom water temperature was recorded to the nearest 0.1°C.

Surveys of this colony were initiated as informal weekly observations beginning in September 1987 and continuing until February 1988. A more rigorous procedure was initiated in March 1988. The study was concluded in September 1989 due to disappearance (presumably harvest) of the entire colony during the first week of September. All observations were carried out using SCUBA. Observation periods varied throughout the day.

The initial weekly observation periods documented cyclic burying and reproductive behavior. One hr observation periods were found to be sufficient to survey the approximately 2000 m^2 area inhabited by the colony. Numbers of individuals buried or not buried, or engaged in spawning or copulation, were recorded and converted to percentages for graphical purposes.

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Beginning in June 1988, conch were tagged for individual identification. Tags consisted of embossed DYMO-brand vinyl tape, numbered consecutively, with a hole punched at one end through which a rubber band was threaded. The rubber band was then wrapped around the spire of the conch and held in place by the spines on the shell. Tag loss was negligible as the rubber bands maintained their integrity for at least the 15-month duration of the tagging portion of the study. Each conch was sexed by observing the foot when extended from the shell: males have verges, and females have egg grooves. A total of 1805 conch were tagged in this colony, of which 1231 were sexed (also see Reed, 1993, for a discussion of sex ratios in this colony); only three juveniles were observed. Those animals used for experimental purposes, such as tank observations (see below), are not included in the 1231 used for field observations. Only 34 tagged conch were found dead during the course of study.

Approximately 100 individuals per hr of observation could be accounted for if tag numbers were recorded. When the entire colony was buried, except for a few, isolated individuals (not engaged in reproductive activity), proportions buried were rounded off to 100% and proportions of reproductively active were set to zero.

The colony was observed on a weekly basis except when spawning was intensive, when observation periods were increased to three per week or more. Activities recorded were: "buried" (conch immersed into the substratum), "unburied" (conch on surface of substratum, and actively moving, with a trail visible behind it, or feeding), "spawning" (egg mass visibly being extruded), and "copulating" (male with verge extended under the shell of the female). Completely buried conch were found by observing the substratum for a protruding eye-stalk. The angle of burial was determined by measuring the depth of the spire of the shell below the surface of the substratum.

Equal numbers of males and females (approximately 25 of each sex at any given time) were collected from the study site as needed and maintained in an outdoor, concrete tank at the laboratory with sandy substratum of 10 cm depth and free-flowing seawater. These conch were also individually tagged and observed daily (including at night) to complement field observations and supplement behavioral data when weather and sea conditions prohibited field activities. Water temperature of the tank was recorded.

Statistical analyses were performed using the SYSTAT package for IBM-PCs (SYSTAT Inc., 1992). Proportions were arc-sine transformed before analysis to ensure homogeneity of variances.

RESULTS

SEASONAL BEHAVIOR

Variations in burial and reproductive activity are summarized in Fig. 1. For both years, the entire colony remained buried for at least two months, starting in mid-November until emerging in late January in 1988 (early February in 1989). Burial during this time period differed from the rest of the year in that conch dug in apex down, and remained at a 45° angle, with only a small hole through which an eye stalk could protrude. The siphonal notch was one cm below the surface of the substratum. The substratum was flat and appeared undisturbed where conch were buried. Occasionally, an individual would emerge and rebury less than a meter away. Because of the cohesive nature of the substratum, original holes and characteristic marks made by the operculum during movement remained in evidence for a week or more.

Winter burial coincided with the annual drop in water temperature for this area, and emergence coincided with the spring equinox and annual rise in water temperature. Bottom water temperature began dropping in the second week of November 1988 from approximately 28°C to 26°C by the third week of December 1988, and remained stable at that temperature until the first week of February 1989, when water temperature began rising. Although no temperature data were recorded at the study site in 1987 and early 1988, a similar drop in water temperature was first noted by divers in November 1987, as was a rise in temperature in February 1988 (later verified from water temperatures recorded at the Department of Marine Sciences, University of Puerto Rico, located approximately 1.5 km away).

Burial during non-winter months was superficial with the conch dug into the substratum, apex down, at a shallower angle of 15° to 30°. The siphonal canal and eye notch(es) of the shell rested level with the substratum.

REPRODUCTIVE PERIODICITY

During the first emergence of the year, no reproductive activity was observed; however, the conch were actively feeding. The second, or "spring," emergence signalled the onset of spawning, which continued on a cyclic basis until the next winter burial. No lag was observed between copulation and onset of spawning in 1988 or 1989, although copulations during the spawning season were frequently observed; first copulations of the season could have occurred outside of the observation times.

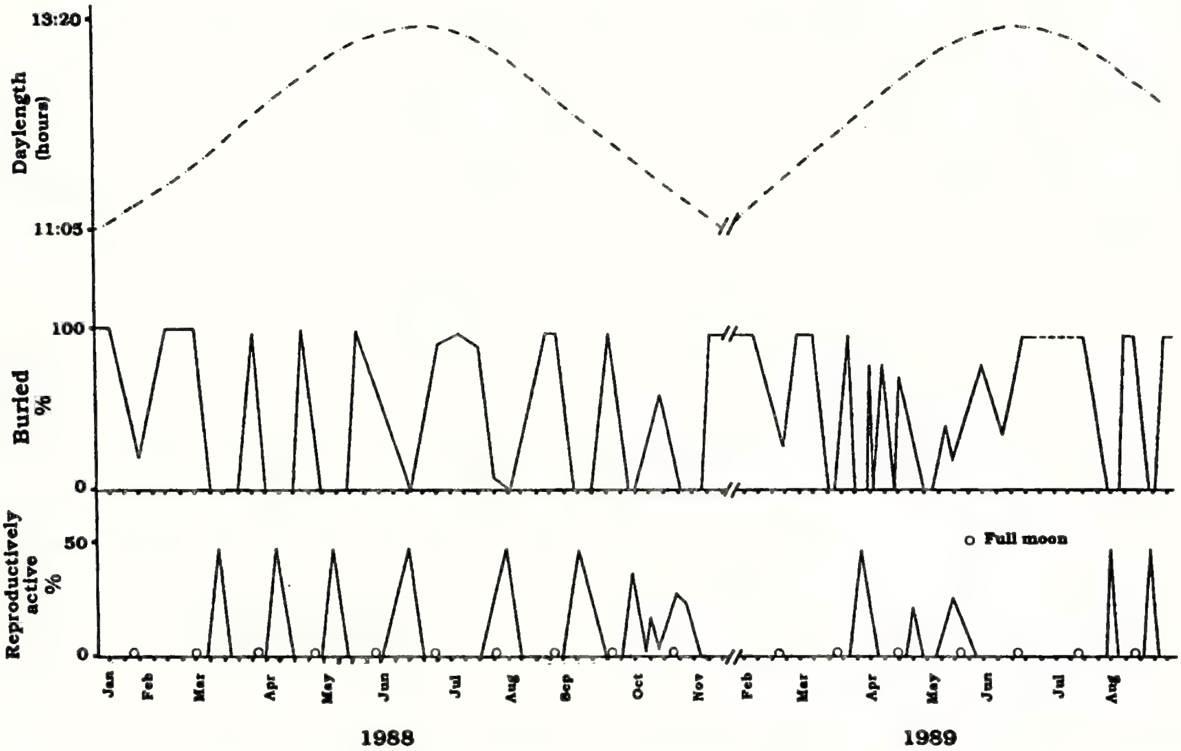

Fig 1. Annual cycle of burial and reproduction in a colony of *Strombus pugilis* in Puerto Rico, from January 1988 to August 1989, including daylength curves and dates of full moons.

Conch maintained in the outdoor tank over winter emerged from the substratum and began reproductive activity concurrently with those in the field; however, relative to the field, water temperature of the tank did not rise. Tank temperature remained constant (23.5°C throughout the winter, until the end of March), and was 3° lower than that in the field (26.5°C).

From March to November, behavior of the colony followed a roughly monthly cycle with week-long spawning peaks. During the fourth week of the cycle, the conch buried superficially. These cycles of behavior were not upset by natural disturbances such as tropical storms, *e.g.* Hurricane Gilbert (12 Sept 1988). However, the conch missed one cycle each year: that which followed the longest day, June 21. No spawning appeared to have taken place anywhere in the study area because egg masses, or remnants thereof, were not found (egg mass remnants usually remained in evidence for up to two weeks after the eggs themselves had hatched). This cyclic reproduction appeared to be associated with the lunar cycle, as spawning peaks were most frequently observed after a full moon. To test the regularity and strength of these cycles, two analyses were made.

To test the regularity of the cycles, a sine wave function was fit to the data using non-linear regression. The model was: $y = a + b * \text{sine}(\text{week} - c)$, where *y* equals the arc-sine transformation of the proportion of individuals reproductively active, and *week* equals the angle equivalent to lunar week (*e.g.* week 1 = 0 radians, week 2 = p/2 radians, etc.); *a* is the shift in the sine function along the y-axis (y-intercept), *b* is the amplitude, and *c* is the phase shift (*a*, *b*, and *c* are constants). The regression was significant ($p < 0.05$) with a = 6.653 ± 1.306 SE, b = 5.645 ± 1.846 SE, and c = 0.007 ± 0.327 SE. Since *c* was small and not significantly different from zero, peak reproductive activity was found to be centered around the second week following the full moon. However, the correlation coefficient was low ($r^2 = 0.400$; $p < 0.05$), indicating that there was variability in the timing and/or strength of the spawning peaks.

Spawning peaked during the second week after a full moon in 10 out of 14 cases (Fig. 1). The strength of these peaks was tested using an analysis of variance (ANOVA), to test for significant differences in the proportion of conch reproductively active (arc-sine transformed) among weeks. The ANOVA results (Table 1) showed a significant difference in mean percentage of spawners on a weekly basis ($p = 0.031$). Reproductive activity was greatest during the second week after a full moon relative to the other three weeks ($p < 0.007$; using post-hoc orthogonal contrasts).

Table 1. Analysis of variance used to test for differences among weeks, with respect to strength of reproductive peaks.

Source	Sum of Squares	Degrees of Freedom	Mean Square	F-ratio	Probability
week	924.101	3	308.034	3.186	0.031
error	5026.929	52	96.672		

DISCUSSION

Reproductive seasonality was observed in *Strombus pugilis*, with all reproductive activity ceasing from mid-November until mid-March. A similar annual cycle of behavior was noted in other colonies of *S. pugilis* located in the general area (Sanders, 1988; pers. obs.), as well as in other strombid species, such as *S. gigas* (*fide* Weil and Laughlin, 1984; pers. obs.), *S. luhuanus* Linné, 1758 (Catterall and Poiner, 1983; Kuwamura *et al.*, 1983), and *S. costatus* (*fide* L. A. Rodríguez Gil, pers. comm.) although the last spawned year-round with variable intensity in Puerto Rico (R. S. Appeldoorn, pers. comm.). Because long-term observations have not been made on populations of the last two species, this type of seasonal behavior is not well documented, and probably differs by locale.

The reproductive season of *Strombus pugilis* coincided with changes in daylength and water temperature. Spring emergence coincided with both increasing daylength and water temperature. Consequently, increasing daylength may be a major factor influencing spring emergence. Stoner *et al.* (1988) also suggested that spring emergence in juvenile *S. gigas* was influenced by increasing daylength and water temperature.

The cessation of reproductive activity and onset of winter burial coincided with both decreasing daylength and water temperature in both the field and the laboratory. In *Strombus gigas*, Stoner *et al.* (1992) found that reproduction gradually decreased with decreasing daylength but ceased altogether when temperature began dropping. The drop in water temperature during the winter also affected metabolic rate in *S. pugilis* (Sanders, 1990), suggesting that cessation of reproduction is determined by energetic requirements, especially because the intensity of reproduction was so high during the season. Low temperature not only reduces the parental metabolic rate but also extends hatching time (Rodríguez Gil *et al.*, 1991) such that larger eggs would have to be produced in winter in order to ensure viability and larval survival (Hughes, 1986). Kuwamura *et al.* (1983) found that the gonadal index of *S. luhuanus* decreased when temperature dropped, and that reproductive activity ceased altogether during winter months in Japan. Given these observations, temperature appears to be the main factor influencing reproductive seasonality in strombids. However, because of the confounding of daylength and temperature in field observations, controlled experiments will be needed to examine the differential effects of daylength and temperature on reproduction.

During the reproductive season, spawning occurred on a monthly basis for *Strombus pugilis*, with a peak in spawning generally falling in the second week after a full moon. Such cyclic behavior could be a response to either internal endogenous rhythms or to external environmental factors, or more likely, a combination of both (Sollberger, 1965). No such periodicity has been reported for other species of *Strombus*.

One possible explanation for the correlation of spawning with lunar periodicity is that larval release (hatching occurs 3-5 days after the egg mass is laid) would occur during the period of neap tides, which could act to restrict the dispersal of larvae to offshore waters where they may perish. From their work in the Grenadines, Posada and Appeldoorn (1994) felt there exists some mechanism limiting dispersal of *Strombus* larvae. However, tidal currents along the south coast of Puerto Rico are exceedingly small (Kjerfve, 1986), so differences between spring and neap tides may not be biologically significant in this particular area, but spawning at certain point(s) during the tidal cycle could have evolved as a mechanism for the retention and transport of larvae to inshore nursery grounds (Posada and Appeldoorn, 1994; Stoner *et al.*, 1992). Using the lunar cycle to cue the periodicity would also serve to ensure that all members of the population were ripe and reproductively active at the same time (Fretter and Graham, 1964).

In the present study, while the reproductive cycle correlated positively with lunar phase, the correlation was imprecise. In four out of 14 cases, spawning peaks did not occur during the second week after a full moon. Furthermore, for both years one spawning cycle was missed, that coincident with the longest day and full moon thereafter, with conch remaining superficially buried for almost a month. Thus, lunar periodicity cannot be seen as the sole factor regulating reproductive activity, but may work in conjunction with, or be influenced by, other as yet undetermined factors.

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The stygobiont genus *Bythiospeum* in Austria: a basic revision and anatomical description of *B.* cf. *geyeri* from Vienna (Caenogastropoda: Hydrobiidae)

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Abstract. The type series of the eight Austrian nominal species of the stygobiont genus *Bythiospeum*, all originally described only from their shells, are compared morphometrically. Two series attributed to *B. geyeri* (Fuchs, 1925) and one sample of an hitherto undescribed species from the type locality of *B. tschapecki* (Clessin, 1878), are also included in this investigation. Several of the taxa have been classified as subspecies or synonyms of other taxa in a variety of combinations. These classifications were based on poorly defined, *i.e.* non-quantified, similarities. It is demonstrated that, in the absence of anatomical data, systematic/taxonomic speculations exclusively based on conchological similarities are pointless and misleading.

In addition, *Bythiospeum* cf. *geyeri* from the groundwater of the river Danube in Vienna is described anatomically. It lacks eyes and epidermal pigment, and is characterized by a number of presumably plesiomorphic (with respect to other hydrobiid genera) features, such as a simple penis, well developed hypobranchial gland, and a duct connecting the prostate and mantle cavity.

The genus *Bythiospeum* Bourguignat, 1882 [synonyms: *Vitrella* Clessin, 1877, non Swainson, 1840; *Lartetia* Boettger, 1905, non Bourguignat, 1869; *Paladilhiopsis* Pavlovic, 1913 (cf. Zilch, 1970; Giusti and Pezzoli, 1982)] is exclusively stygobiont. It comprises more than 100 nominal species and subspecies and is reported from the Netherlands throughout western and central Europe, the Balkans, Asia minor, to the Caucasus and Usbekistan (Boettger, 1905; Bole and Velkovrh, 1986; Kuijper and Gittenberger, 1993). The great majority of these nominal species and subspecies has been only vaguely described from shells and there is great confusion as to possible synonymies, because shell characters provide little information for hydrobiid systematics. A comprehensive revision of the genus would have to be based on exact morphometric descriptions and, primarily, on anatomical investigations. However, stygobiont hydrobiids are rarely encountered alive, which is rather discouraging if one considers the great number of taxa. Thus, it is not surprising that the few revisionary papers concentrate on limited geographic areas. Boeters (1984b) developed some ideas for the revision of the German species and Bernasconi (1990) focused on France, Switzerland, and also Germany.

The recent discovery of a considerable number of living specimens of *Bythiospeum* cf. *geyeri* (Fuchs, 1925) in the groundwater of the river Danube in Vienna gave rise to a revision of the eight Austrian taxa: *B. tschapecki* (Clessin, 1878), *B. pfeifferi* (Clessin, 1890), *B. geyeri*, *B. elseri* (Fuchs, 1929), *B. noricum* (Fuchs, 1929), *B. bormanni* (Stojaspal, 1978), *B. cisterciensorum* (Reischütz, 1983), and *B. reisalpense* (Reischütz, 1983). Throughout a series of papers, Reischütz (1981, 1983a, b, c) considered only *B. tschapecki* and *B. pfeifferi* as valid species. The other taxa were treated either as species, subspecies (in a variety of combinations), or synonyms. Reischütz's argument was based on conchological comparisons, but his argumentation is not convincing, because it lacks any quantification.

The present paper provides a morphometric analysis including the type series of the nominal Austrian species of the genus *Bythiospeum*, presumptive topotypes of *B. pfeifferi*, a series of two populations attributed to *B. geyeri* by previous authors (*e.g.* Klemm, 1960; Pospisil, 1989; Reischütz, 1988b), and one lot of an undescribed species from the type locality of *B. tschapecki*, with which it has been confused by Reischütz (1983b). The anatomy of *B.* cf. *geyeri* from the groundwater of the river Danube in Vienna is described in full detail and its evolutionary significance discussed.

MATERIALS AND METHODS

Part of Clessin's collection including the type series of *Bythiospeum pfeifferi* deposited in the State Museum of Natural History in Stuttgart (SMNS) was destroyed during

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World War II (Zilch, 1970; Niederhöfer, pers. comm.). But four shells of Clessin's original material of *B. pfeifferi* still exist in the Museum of Natural History in Vienna (NHMW). For the species described by Fuchs and Clessin, lecto- and paralectotypes are designated from the syntypic series. All series except that of *B.* cf. *geyeri* from well T3 in Vienna consist of empty shells collected in caves, wells, springs and riverine alluvia.

Material examined (see Fig. 1 for localities):

Bythiospeum bormanni: coll. Reischütz: cave Bärenloch near Mixnitz.

B. cisterciensorum: NHMW 82577: spring in Siebenbrunn/Türnitz.

B. elseri: lectotype: NHMW 87187; paralectotypes: NHMW 33180: Gresten; [NHMW/K 48830: Traun near Wels, 1 shell, not used in this analysis].

B. geyeri: lectotype: NHMW 87186; paralectotypes: NHMW/K 6815, NHMW/E 33143, NHMW/E 33144, NHMW 53279: all from Eichhornquelle (Quelle = spring) in Schönbühel/Donau; coll. Rusnov, NHMW/E 1630, NHMW/K 44000: all alluvium of the Danube in Schönbühel.

B. cf. *geyeri:* NHMW 5276: Weidlingbach; well T3 at the Eberschüttwasser in Vienna.

B. noricum: lectotype: NHMW 87188; paralectotypes: NHMW/K 48785: Gaflenz in Weyer/Enns.

B. pfeifferi: lectotype: NHMW 87189; paralectotypes: NHMW 22382; presumptive topotypes: NHMW 29471, NHMW/E 1622, NHMW/K 48826: all Kremsmünster.

B. reisalpense: NHMW 82576: spring in Kleinzell.

B. tschapecki: lectotype: SMNS ZI 9429/1; paralectotypes: SMNS ZI 9429/2-4; Buchkogelhöhle near St. Martin.

B. sp.: coll. Reischütz: Buchkogelhöhle near St. Martin.

Shells were measured with a dissecting microscope fitted with an ocular micrometer. Only shells with a fully developed peristome were used (cf. Fig. 8A). Parameters measured included shell height (sh), shell width (sw), aperture height (ah), and aperture width (aw). In addition, the ratios sh:sw, ah:aw, sh:ah and sw:aw were calculated. The means and the confidence intervals of the means ($p = 0.05$) of all eight parameters were plotted to sun ray diagrams, whose axes are limited by the respective minima and maxima. Differences among series are considered statistically significant if the confidence intervals do not overlap. In addition, pairwise Euclidean distances between the series were calculated from the z-transformed means of each variable. Cluster analyses [Unweighted Pair Group Method using Arithmetic averaging; UPGMA] and minimum spanning trees were computed based on all eight parameters (overall similarity) and on the four ratios (shape), respectively. UPGMA cluster analysis was carried out using the program NEIGHBOR of Felsenstein's (1993) package PHYLIP, version 3.5c. NEIGHBOR generates UPGMA dendrograms with half the branch lengths produced by the usually used algorithm of Sneath and Sokal (1973). Therefore, the branch lengths computed by NEIGHBOR were multiplied by two. The program SLINK, employing a single-linkage algorithm, written by Dr. Nemeschkal (Vienna), was used to generate the minimum spanning trees. Discriminant analysis and analysis of variance could

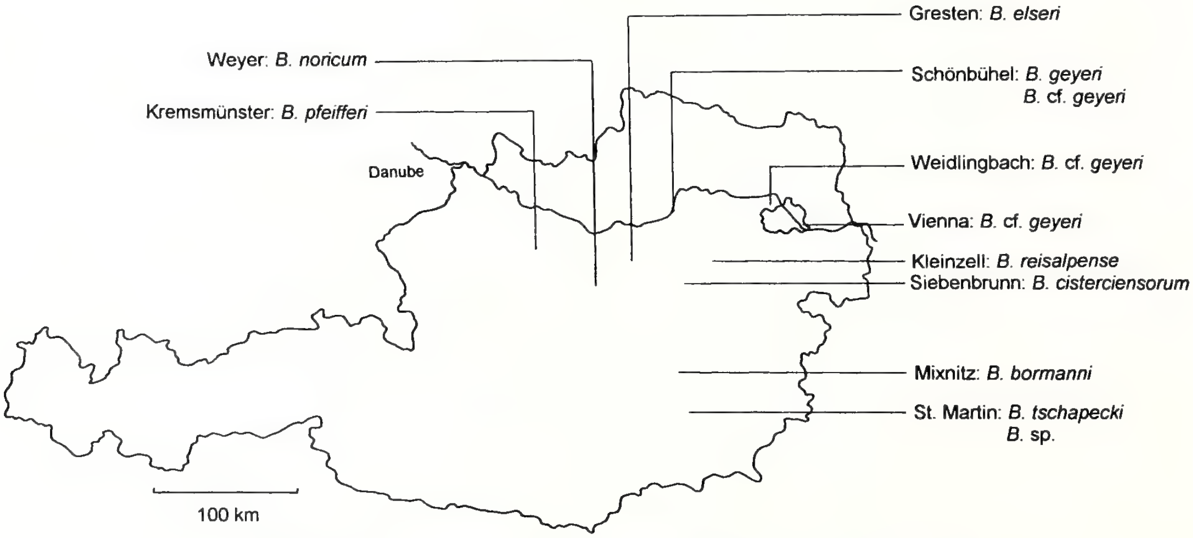
Gresten: B. elseri
Weyer: B. noricum
Schönbühel: B. geyeri
B. cf. geyeri
Kremsmünster: B. pfeifferi
Danube
Weidlingbach: B. cf. geyeri
Vienna: B. cf. geyeri
Kleinzell: B. reisalpense
Siebenbrunn: B. cisterciensorum
Mixnitz: B. bormanni
St. Martin: B. tschapecki
B. sp.
100 km

Fig. 1. Map of Austria showing the localities of the series investigated in this study.

not be performed because the variances of the measurements are not homogeneous (Bartlett's test).

The living specimens of *Bythiospeum* cf. *geyeri* (11 females, 3 males) were collected with a double-packer sampler connected to a hand-pump (Danielopol and Niederreiter, 1987) in the groundwater monitoring well T3 (a pipe with a diameter of 4.8 cm) near the Eberschüttwasser, a backwater of the river Danube, in Vienna, Austria, from a depth of 10-12 m by Dr. P. Pospisil in September 1992. The animals were fixed unrelaxed with Bouin's fixative. Eight females and two males were embedded in paraffin and sectioned at 7 µm. The serial sections were stained with Heidenhain's Azan. The anatomy was reconstructed from the series of one female and one male using the computer program PC3D (Jandel Scientific). Two females and one male were dissected. The head-foot of the male was critical-point dried after removal of the mantle and investigated with a scanning electron microscope (SEM). One radula and representative shells were also examined with the SEM. All of these methods are described in more detail in Haase (1992).

RESULTS

MORPHOMETRICS

The shell measurements of all species and populations investigated are given in Table 1. The series from the Eichhornquelle, Schönbühel (both *Bythiospeum geyeri*) and Kremsmünster (*B. pfeifferi*, collected by Pfeiffer), respectively, were pooled in order to increase the number of specimens for the analysis. This is justified because Fuchs's and Pfeiffer's original series were partly distributed among several collectors (indicated by the lables; Wawra, pers. comm.), whose collections are now deposited in NHMW.

Shell parameters of the four populations of *B. geyeri* (including *B.* cf. *geyeri*) are compared in Fig. 2. The significant differences are summarized in Table 2.

Shell parameters of the type series of the Austrian species of *Bythiospeum* (with *B. geyeri* represented by the series from the Eichhornquelle) and *B.* sp. from St. Martin are contrasted in Fig. 3. The significant differences of Fig. 3 are summarized in Table 3. *Bythiospeum elseri*, *B. geyeri* and *B. noricum* differ only in size parameters. *B. pfeifferi* can also be distinguished from *B. geyeri* and *B. noricum* only in size. The same holds for comparison of *B. tschapecki* with *B. geyeri* and *B. noricum*, and *B.* sp. with *B. elseri*. *B. tschapecki* and *B. pfeifferi* cannot be distinguished at all. However, one has to be careful drawing conclusions from Figs. 2 and 3, because several samples contain only a few specimens, which results in quite large confidence intervals and thus less clear separation between the series.

Figs. 4 and 5 show UPGMA phenogram and a minimum spanning tree, respectively, based on the Euclidean distances in Table 4 considering size and shape parameters. Figs. 6 and 7 are based on the shape parameters only. These dendrograms and minimum spanning trees are dealt with in more detail in the Discussion.

DESCRIPTION OF *BYTHIOSPEUM* CF. *GEYERI* FROM VIENNA

SHELL

The shell (Fig. 8) is unsculptured and comprises up to five whorls. The outer lip is curved (Fig. 8B). The protoconch (Fig. 8C) is smooth and has 1.5 whorls. Measurements are given in Table 1.

OPERCULUM

The light orange operculum is paucispiral with an excentric nucleus.

EXTERNAL FEATURES

The epidermis is unpigmented. Yellow granules lie in the musculature and connective tissue of the foot. Black granules are dispersed in the connective tissue around the stomach and the distal lobes of the digestive gland (Fig. 9). These black granules lie close to the nuclei of the cells of the connective tissue, which have large vacuoles. The snails have no eyes, not even rudiments. The tentacles bear a median row of cilia (Fig. 10).

MANTLE CAVITY EXCEPT DISTAL GENITAL ORGANS

The ctenidium consists of 14-16 filaments. The hypobranchial gland is very massive and extends almost the full length of the pallial oviduct (Fig. 11A). In the roof of the mantle cavity the intestine forms a loop, which is about half as long as the albumen gland in most specimens. Some individuals, such as the one depicted in Fig. 11A, have a somewhat shorter loop.

DIGESTIVE SYSTEM

The radula (Fig. 12) includes more than 100 rows and is described by the formula R: $\frac{5\ 1\ 5}{1\ 1}$, L: 4 1 4, M_1: 18 - 21, M_2: 16 - 19. Esophagus and digestive gland open side-by-side into the proximal end of the stomach, which is bent toward the digestive gland. Stomach and digestive gland are not very close and are connected via a duct. The digestive gland is a large sac with four to five prominent, distal lobes (Fig. 13).

NERVOUS SYSTEM

The cerebral and pleural ganglia are separated by short, but distinct, connectives so that the ganglia are not

Table 1. Shell morphometry; measurements in mm, s*100/x̄ in %. (ah, aperture height; aw, aperture width; max, maximum; min, minimum; N, number of specimens; s, standard deviation; s*100/x̄, coefficient of variation; sh, shell height; sw, shell width; w, maximum number of whorls; x̄, mean).

		sh	sw	ah	aw	sh:sw	ah:aw	sh:ah	sw:aw
B. bormanni	min	1.73	0.85	0.63	0.58	1.95	0.96	2.74	1.36
Mixnitz	max	2.03	1.03	0.70	0.68	2.32	1.13	2.93	1.58
N = 17	x̄	1.87	0.91	0.66	0.62	2.07	1.06	2.83	1.46
w = 4.75	s	0.09	0.05	0.02	0.03	0.10	0.05	0.07	0.08
	s*100/x̄	4.58	4.95	3.56	4.36	4.84	4.36	2.28	5.14
B. cisterciensorum	min	2.03	1.13	0.93	0.88	1.67	1.03	2.14	1.25
Siebenbrunn	max	2.58	1.45	1.13	1.08	1.80	1.06	2.29	1.40
N = 4	x̄	2.23	1.26	1.01	0.96	1.76	1.05	2.21	1.31
w = 4.75	s	0.25	0.14	0.10	0.09	0.06	0.01	0.06	0.08
	s*100/x̄	11.42	10.79	9.81	9.60	3.42	1.20	2.77	5.70
B. elseri	min	1.75	0.75	0.58	0.50	2.25	1.14	3.00	1.43
Gresten	max	2.10	0.83	0.65	0.55	2.55	1.24	3.36	1.57
N = 7	x̄	1.90	0.79	0.61	0.52	2.40	1.17	3.11	1.51
w = 4.7	s	0.11	0.03	0.02	0.02	0.11	0.04	0.13	0.05
	s*100/x̄	5.92	4.03	4.00	3.31	4.54	3.30	4.14	3.01
B. geyeri	min	2.23	0.93	0.75	0.65	2.19	1.11	2.68	1.34
Eichhornquelle	max	2.60	1.08	0.93	0.80	2.60	1.19	3.15	1.54
N = 8	x̄	2.38	1.03	0.81	0.70	2.33	1.16	2.94	1.47
w = 5.5	s	0.12	0.05	0.05	0.05	0.13	0.03	0.13	0.07
	s*100/x̄	5.20	4.88	6.58	6.61	5.46	2.35	4.56	4.51
B. cf. *geyeri*	min	1.90	0.78	0.63	0.50	2.03	1.14	2.61	1.39
Schönbühel	max	2.45	1.08	0.88	0.70	2.45	1.26	3.04	1.58
N = 15	x̄	2.20	0.97	0.79	0.65	2.27	1.22	2.80	1.50
w = 5.25	s	0.15	0.07	0.06	0.05	0.11	0.04	0.12	0.06
	s*100/x̄	7.01	6.89	7.59	8.12	4.97	3.30	4.39	3.88
B. cf. *geyeri*	min	1.83	0.83	0.65	0.53	2.14	1.11	2.69	1.39
Vienna, T3	max	2.48	1.08	0.90	0.75	2.46	1.28	3.11	1.61
N = 15	x̄	2.17	0.94	0.76	0.63	2.30	1.21	2.84	1.49
w = 5.0	s	0.19	0.07	0.06	0.06	0.09	0.05	0.11	0.07
	s*100/x̄	8.87	7.39	8.38	9.51	4.03	3.71	3.93	4.52
B. cf. *geyeri*	min	1.68	0.75	0.58	0.48	2.16	1.11	2.75	1.43
Weidlingbach	max	2.30	1.00	0.80	0.70	2.58	1.29	3.15	1.58
N = 10	x̄	2.03	0.86	0.69	0.58	2.37	1.19	2.96	1.49
w = 5.0	s	0.21	0.09	0.08	0.07	0.15	0.06	0.12	0.06
	s*100/x̄	10.08	10.45	11.27	12.82	6.30	4.88	3.92	3.94
B. noricum	min	1.88	0.85	0.60	0.53	2.03	1.14	2.77	1.50
Weyer	max	2.28	1.05	0.78	0.65	2.42	1.25	3.13	1.76
N = 5	x̄	2.06	0.94	0.70	0.59	2.21	1.20	2.95	1.60
w = 5.5	s	0.17	0.07	0.07	0.05	0.14	0.04	0.16	0.10
	s*100/x̄	8.39	7.93	9.78	8.33	6.38	3.64	5.56	6.22
B. pfeifferi	min	2.25	0.92	0.78	0.64	2.08	1.07	2.48	1.29
Kremsmünster	max	3.08	1.31	1.11	0.97	2.49	1.25	3.20	1.63
N = 20	x̄	2.59	1.16	0.92	0.80	2.23	1.15	2.82	1.46
w = 5.0	s	0.23	0.10	0.09	0.09	0.11	0.05	0.16	0.10
	s*100/x̄	8.91	8.25	10.13	11.15	5.04	4.20	5.75	6.91
B. reisalpense	min	1.70	0.90	0.70	0.63	1.74	1.07	2.27	1.39
Kleinzell	max	2.60	1.20	0.98	0.85	2.17	1.24	2.67	1.56
N = 13	x̄	2.04	1.05	0.82	0.73	1.93	1.13	2.48	1.45
w = 5.25	s	0.23	0.09	0.08	0.07	0.11	0.05	0.12	0.05
	s*100/x̄	11.42	8.55	9.96	9.15	5.92	4.43	4.75	3.60
B. sp.	min	2.08	0.92	0.67	0.56	2.19	1.09	3.13	1.48
St. Martin	max	2.53	1.03	0.78	0.64	2.68	1.22	3.38	1.70
N = 5	x̄	2.31	0.97	0.70	0.61	2.37	1.16	3.28	1.61
w = 5.5	s	0.17	0.05	0.05	0.03	0.18	0.05	0.11	0.08
	s*100/x̄	7.15	4.78	6.91	5.35	7.65	3.99	3.40	5.01
B. tschapecki	min	2.59	1.15	0.95	0.82	1.89	1.14	2.72	1.31
St. Martin	max	3.41	1.80	1.18	1.02	2.37	1.23	2.91	1.77
N = 4	x̄	3.00	1.38	1.07	0.91	2.21	1.17	2.81	1.51
w = 5.25	s	0.34	0.29	0.10	0.09	0.22	0.04	0.10	0.20
	s*100/x̄	11.23	21.21	8.88	9.92	9.86	3.44	3.54	13.42

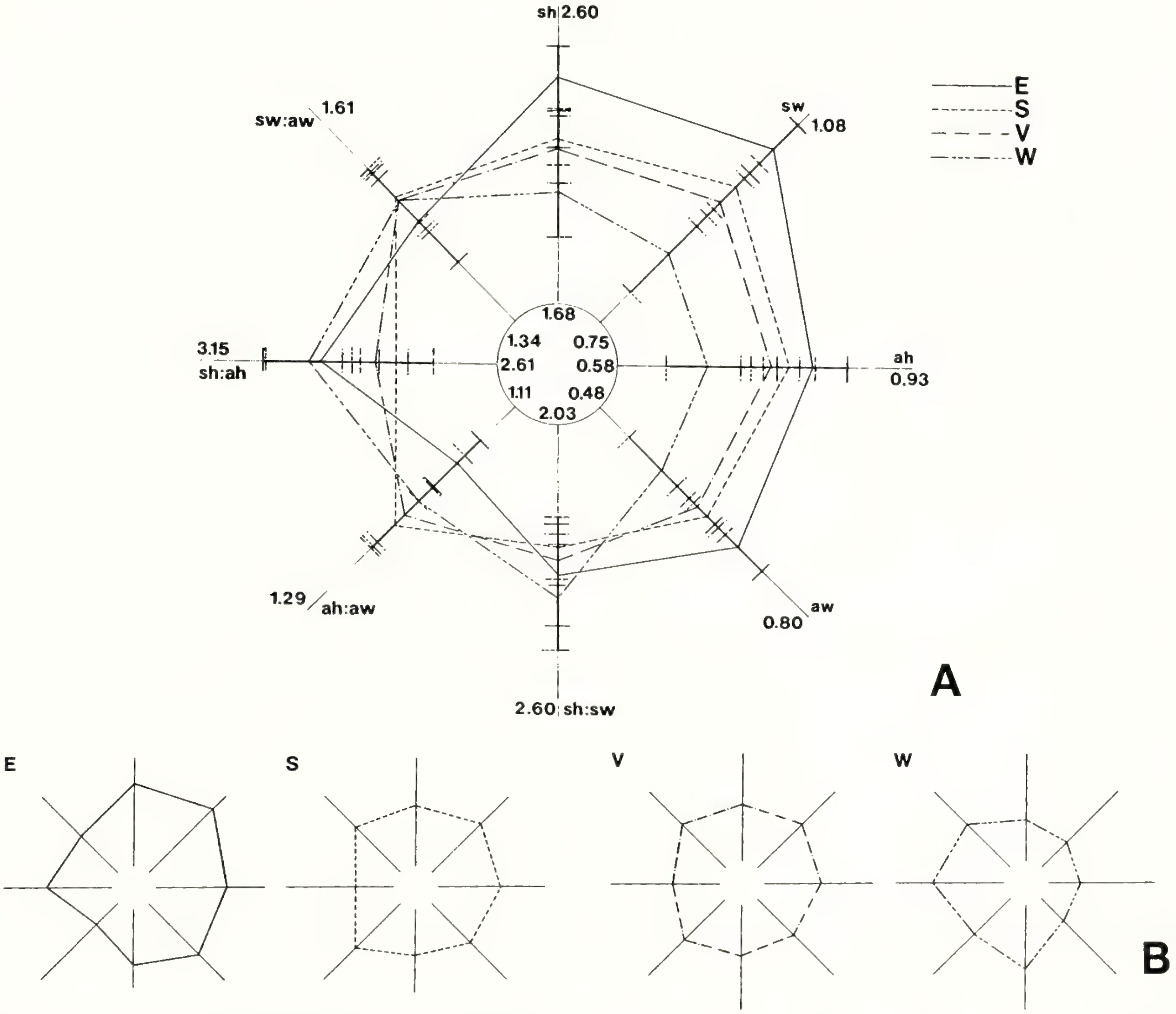

Fig. 2. Sun ray diagrams comparing shell parameters in the four series of, or attributed to, *Bythiospeum geyeri*. **A.** Comparison of all four series. **B.** Each series on a separate diagram. The means of the variables of each series are connected; in A the confidence intervals are also plotted on the axes, which are limited by the respective maxima and minima. The series are identified by the initial letter of their respective locality. (ah, aperture height; aw, aperture width; E, Eichhornquelle; S, alluvium of the river Danube in Schönbühel; sh, shell height; sw, shell width; V, Vienna; W, Weidlingbach.)

fused. The pleurosupraesophageal connective is much longer than the pleurosubesophageal connective. The tentacle nerves arise from a ganglionic thickening at the distal end of the cerebral ganglia.

FEMALE GENITAL SYSTEM (FIGS. 11, 13A)

The ovary is a simple sac. The glandular, renal oviduct makes a wide loop. The gonopericardial duct branches off at the proximal end of the renal oviduct. It cannot be determined from sections whether this is still an open duct or a massive strand of tissue. Albumen and capsule glands are both divided into two histologically differently staining sections. The genital chamber lies behind the albumen gland. The former is inclined towards the latter. The seminal receptacle is ventral to the bursa copulatrix.

MALE GENITAL SYSTEM (FIGS. 10, 14)

The testis is a simple sac. The seminal vesicle is weakly developed with only a few coils. The proximal vas deferens opens into the prostate near its posterior end. The distal vas deferens originates close to its tip. The penis is simple; it has no appendages, neither muscular nor glandular. The prostate overlies the mantle cavity only by its anterior third; it is connected to the mantle cavity through a duct, which arises somewhat behind the distal vas deferens.

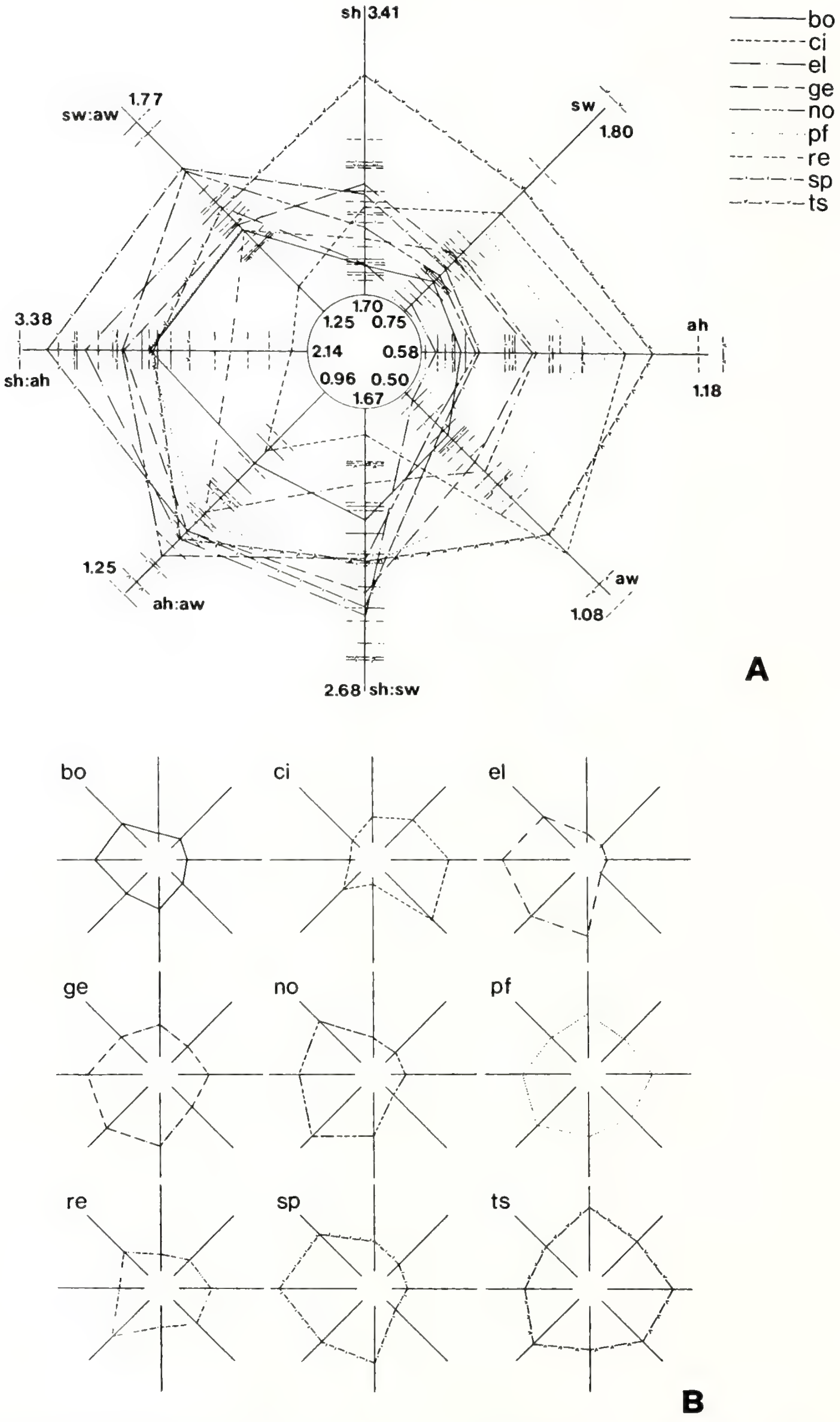

Fig. 3. Sun ray diagrams contrasting shell parameters in the type series of the Austrian taxa of *Bythiospeum* and *B.* sp. from St. Martin; **A.** Comparison of all nine series. **B.** Each series on a separate diagram; the series are identified by their first two initials, see also legend of Fig. 2. (bo, *B. bormanni*; ci, *B. cisterciensorum*; el, *B. elseri*; ge, *B. geyeri*; no, *B. noricum*; pf, *B. pfeifferi*; re, *B. reisalpense*; sp, *B.* sp.; ts, *B. tschapecki*)

Table 2. Significantly different shell parameters extracted from Fig. 2. The parameters are abbreviated by numbers: 1, sh; 2, sw; 3, ah; 4, aw; 5, sh:sw; 6, ah:aw; 7, sh:ah; 8, sw:aw.

	E	S	V	W
Eichhornquelle (E)	—	6	1,2,6	1-4
Schönbühel (S)		—	—	2,3,7
Vienna (V)			—	—
Weidlingbach (W)				—

DISCUSSION

TAXONOMY

The generic allocation of the Austrian species follows Giusti and Pezzoli (1982), who synonymized *Bythiospeum* Bourguignat, 1882, and *Paladilhiopsis* Pavlovic, 1913. Bernasconi's (1990) distinction between these nominal genera is not convincing.

Bythiospeum pfeifferi (originally *Vitrella pfeifferi* Clessin, 1890) is usually cited with the date 1887 (Ehrmann, 1933; Klemm, 1960; Reischütz, 1981; Bole and Velkovrh, 1986). However, Clessin's opus appeared in several parts, the last one (1890) containing the description of this species (Boeters, 1967). In the same year, Pfeiffer (1890) reported observations on living specimens he kept in an aquarium, describing the habitus of the snails. Pfeiffer, who left the first description of shells of this species to Clessin and who knew the page proofs of Clessin's opus, attributed the taxon to Clessin, but his description is independent and does not cite Clessin. Also in 1890 Westerlund (1890) published a description of "*Paludina (Bythiospeum) pfeifferi* Clessin," but he unambiguously copied Clessin's description and also referred to the latter. Thus, Westerlund is certainly not the author of *B. pfeifferi.* Both Clessin's and Pfeiffer's contributions appeared early in 1890, although the exact dates could not be determined. Following the principle of the first reviser (Article 24; ICZN, 1985), I give precedence to *Vitrella pfeifferi* Clessin over *V. pfeifferi* Pfeiffer, because this taxon has never been used in conjunction with Pfeiffer, and because Pfeiffer himself attributed the authorship to Clessin.

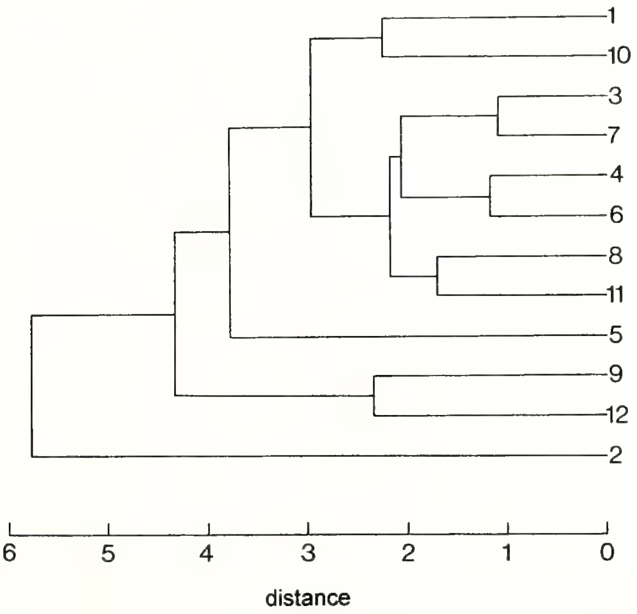

Fig. 4. UPGMA dendrogram based on Euclidean distances in Table 4 considering all eight shell parameters; the series are numbered as in Table 4.

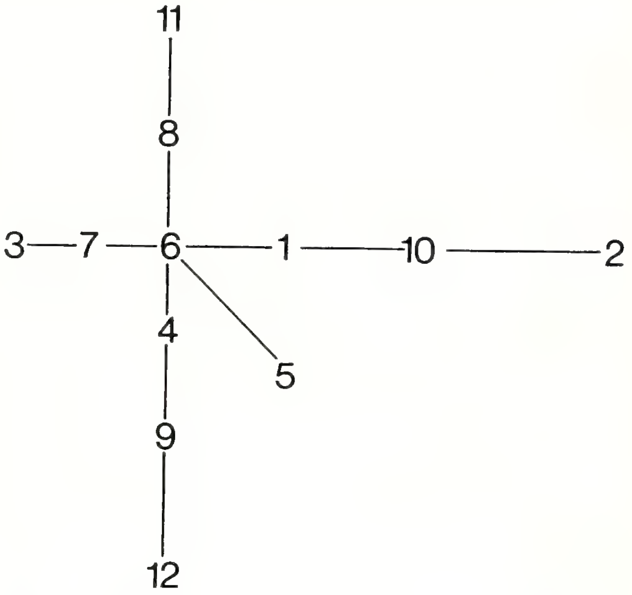

Fig. 5. Minimum spanning tree based on the same data set as Fig. 4; branch lengths are proportional to distances.

MORPHOMETRICS

It is interesting to note that the coefficients of variation (s*100/x̄) of the measurements in most cases exceed 6.5%, whereas they are mostly below 6% for the ratios (Table 1). In species of the hydrobiid genera *Belgrandiella* Wagner, 1828, and *Graziana* Radoman, 1975, Haase (1994) found significantly less variation in size. For the pulmonate *Arianta arbustorum* (Linné, 1758), Baur (pers. comm.) suggested that a value less than 5% can be considered typical for a population. Higher variation might indicate that the sample consists of individuals of two or more populations. The results for the series measured in this study allow two possible conclusions. Either (most) populations of *Bythiospeum* species are more variable in size than those of other gastropods, or (most or some of) the series contain individuals of at least two populations or species, which are very similar in shape. At least for the alluvial samples, the latter explanation seems quite plausible. In fact, Fuchs' (1929) material of *B. noricum* (NHMW/K 48 785) is appar-

Table 3. Significantly different shell parameters extracted from Fig. 3; parameters abbreviated by numbers 1 to 8 as in Table 2.

	bo	ci	el	ge	no	pf	re	sp	ts
B. bormanni (bo)	-----	2-5,7	2-7	1,3-6	6	2-6	2-7	1,5-8	1,3,6
B. cisterciensorum (ci)		-----	2-8	4-7	2-8	5-7	4-7	2-8	5,6
B. elseri (el)			-----	1-4	2	1-5,7	2-5,7	1-4	1-4,7
B. geyeri (ge)				-----	4	1-4	1,5,7	3,4,7	1,3,4
B. noricum (no)					-----	1-4	4,5,7	7	1,3,4
B. pfeifferi (pf)						-----	1-3,5,7	2-4,7,8	-----
B. reisalpense (re)							-----	3-5,7,8	1,3,7
B. sp. (St. Martin) (sp)								-----	3,4,7
B. tschapecki (ts)									-----

ently composed of two species, of which one, represented by two shells, was excluded from the analysis along with one specimen from Reischütz's (1983b) material of "*B. tschapecki*" (here *B.* sp., the specimen excluded is probably a true *B. tschapecki*). [The two shells separated from the *B. noricum* series and *B.* sp. from St. Martin probably represent undescribed species. However, I refrain from describing new species based solely on shell morphology, because this only increases the number of poorly defined taxa in this genus (see also discussion below).] However, the anatomical investigation of the series attributed to *B. geyeri* from Vienna (s*100/x̄ > 7% for the size parameters) did not indicate the presence of more than one species in the drainage area of well T3. This sample certainly represents a single population, which in turn, supports the first assumption, that populations of *Bythiospeum* can be quite variable.

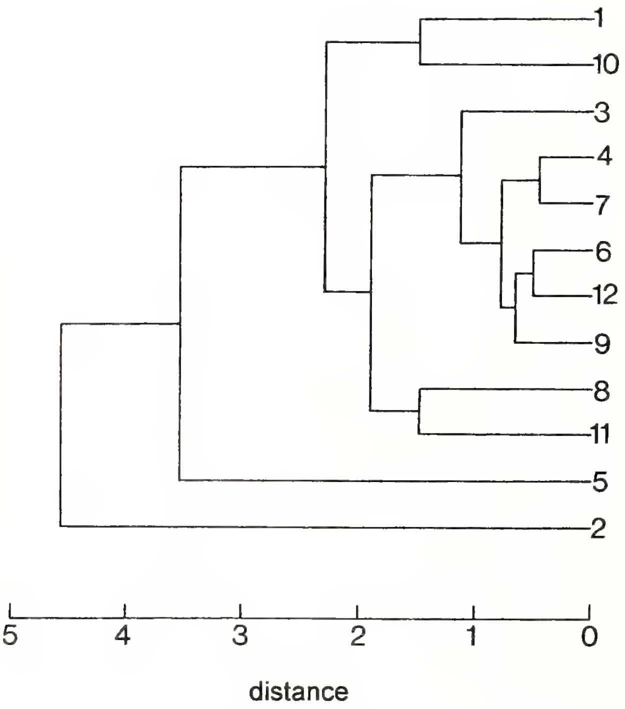

Fig. 6. UPGMA dendrogram based on Euclidean distances in Table 4 considering only shape parameters; the series are numbered as in Table 4.

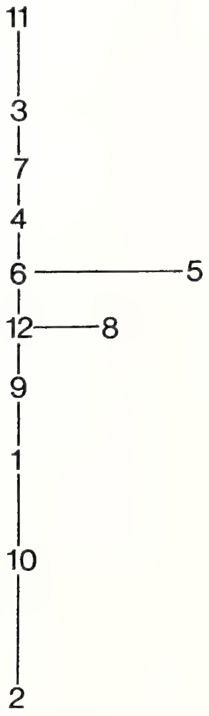

Fig. 7. Minimum spanning tree based on the same data set as Fig. 4; branch lengths are proportional to distances.

In his first review of Austrian species of the genus *Bythiospeum*, Reischütz (1981) ranked all hitherto described taxa as separate species, but suspected that only *B. geyeri* and *B. pfeifferi* were valid. He also speculated that the Austrian taxa might be closely related to *B. acicula* (Held, 1837) from the groundwaters of the river Isar near Munich. [*Paludina acicula* Held, 1837, was not included in this investigation because the syntypes are lost (*fide* Zilch, 1970) and the name itself is dubious, probably preoccupied by *Acmea acicula* Hartmann, 1821 (cf. Boeters, 1984b). Hence, it does not make sense to speculate about relationships of the Austrian taxa to a German species at the present state of revision of the German taxa (cf. Boeters,

Table 4. Matrix of Euclidean distances calculated from z-transformed means of each variable; above the diagonal: all eight parameters; below: only the ratios (see Table 1); the populations of *Bythiospeum geyeri* are distinguished by the initials of their localities. (E = Eichhornquelle, S = Schönbühel, V = Vienna, W = Weidlingbach).

	1	2	3	4	5	6	7	8	9	10	11	12
1. *B. bormanni*	-----	5.391	2.473	2.603	4.221	1.906	1.958	2.323	3.645	2.273	3.389	5.865
2. *B. cisterciensorum*	3.352	-----	7.513	5.276	6.603	5.631	6.542	6.653	4.267	3.446	7.421	4.899
3. *B. elseri*	2.221	5.403	-----	3.001	4.078	2.183	1.103	2.084	4.590	4.367	2.357	6.705
4. *B. geyeri* E	1.491	4.475	0.968	-----	3.466	1.175	1.994	2.506	1.625	2.869	2.495	3.820
5. *B.* cf. *geyeri* S	3.981	5.720	3.501	3.370	-----	3.080	3.436	3.586	4.088	4.199	4.097	5.538
6. *B.* cf. *geyeri* V	1.478	4.396	1.162	0.571	3.071	-----	1.106	1.697	2.571	2.638	2.327	4.743
7. *B.* cf. *geyeri* W	1.831	4.866	0.624	0.462	3.225	0.584	-----	1.717	3.565	3.468	2.186	5.732
8. *B. noricum*	2.205	5.277	1.648	1.900	3.474	1.560	1.653	-----	3.664	3.374	1.700	5.475
9. *B. pfeifferi*	0.935	3.843	1.566	0.668	3.415	0.669	1.034	1.980	-----	2.845	3.685	2.342
10. *B. reisalpense*	1.499	2.309	3.446	2.642	4.087	2.391	2.930	3.006	1.980	-----	4.513	4.668
11. *B.* sp.(St. Martin)	3.058	6.373	1.374	2.235	4.030	2.230	1.881	1.488	2.675	4.232	-----	5.241
12. *B. tschapecki*	1.138	4.147	1.464	0.912	3.258	0.513	0.998	1.370	0.659	2.028	2.311	-----

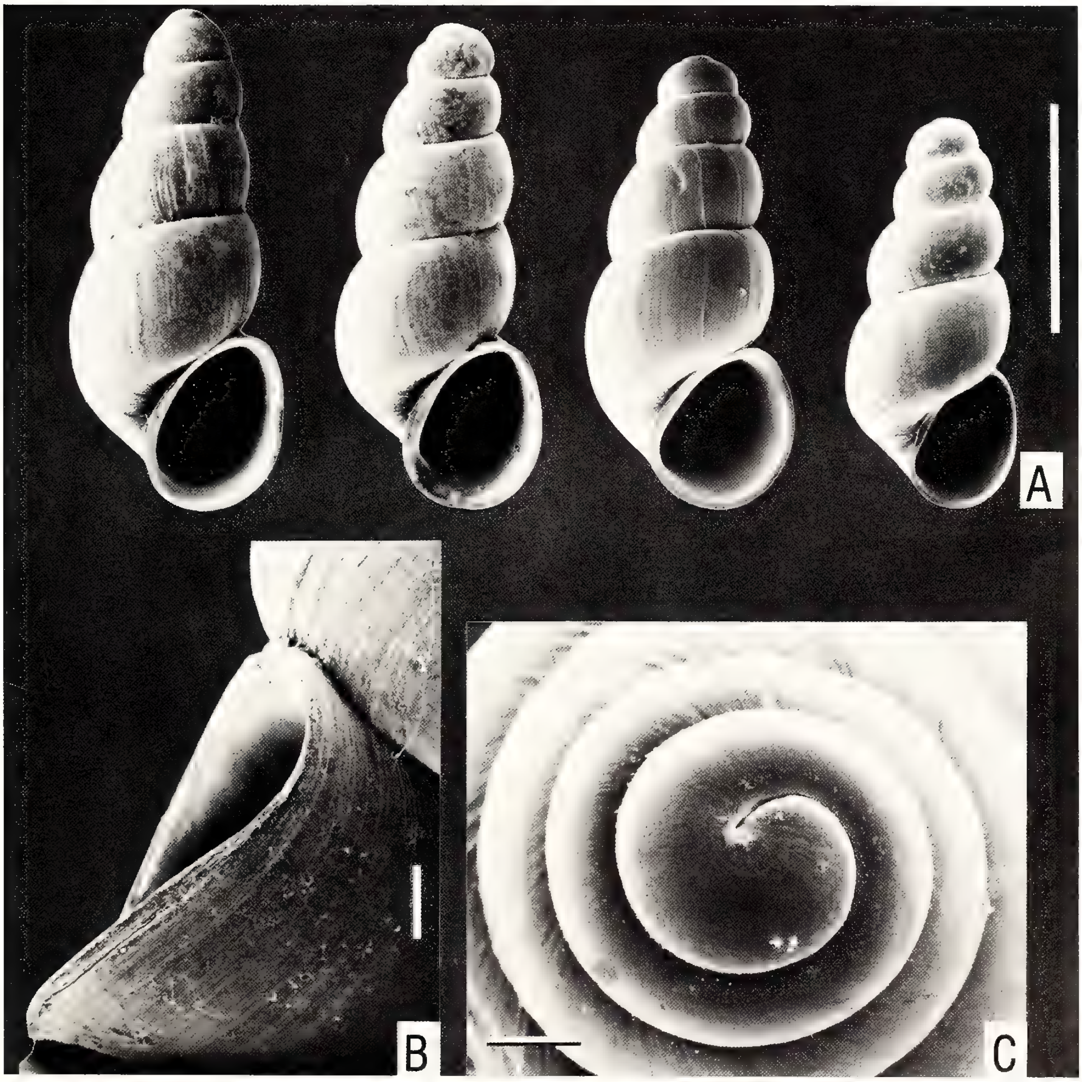

Fig. 8. *Bythiospeum* cf. *geyeri* from Vienna (SEM). **A.** Shells, the right one from a subadult specimen. **B.** Outer lip. **C.** Apical view. Scale bars = 1 mm (A); 100 µm (B,C).

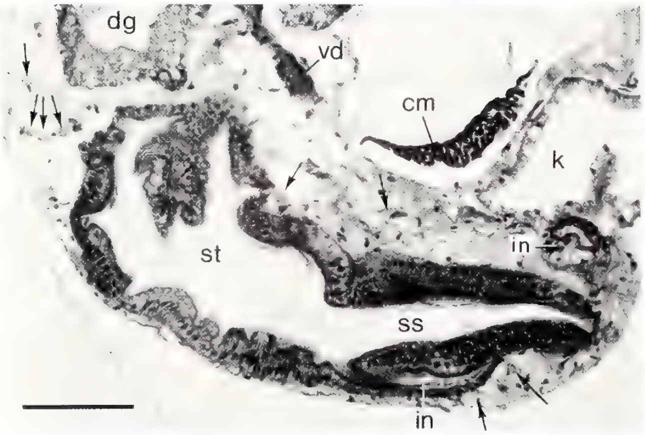

Fig. 9. *Bythiospeum* cf. *geyeri* from Vienna; longitudinal section through the stomach. Arrows indicate dark granules in the connective tissue. (cm, columellar muscle; dg, digestive gland; in, intestine; k, kidney; ss, style sac; st, stomach.) Scale bar = 100 µm.

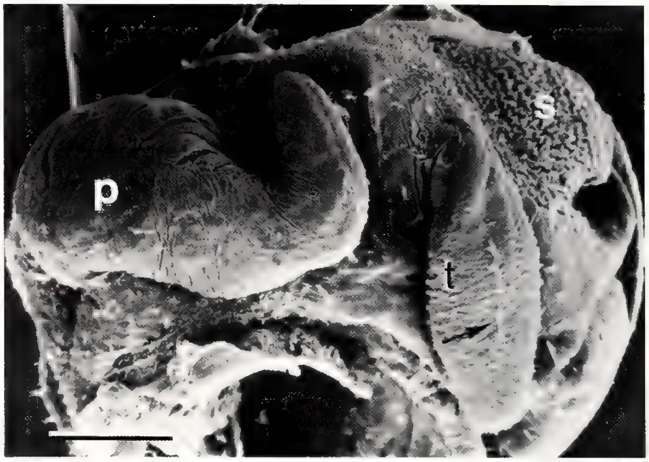

Fig. 10. *Bythiospeum* cf. *geyeri* from Vienna; SEM micrograph of a male, with mantle cavity removed. Arrow indicates dorsomedian row of cilia on the tentacle. (s, snout; p, penis; t, tentacle.) Scale bar = 100 mm.

1984b; Bernasconi, 1990).] In 1983 (Reischütz, 1983a), *B. elseri* became a synonym, and *B. noricum* a subspecies, of *B. geyeri* without any comment. In the same paper Reischütz stated that stunted forms of *B. cisterciensorum* and *B. reisalpense* approach *B. geyeri.* Some months later, Reischütz (1983b) assumed that the Austrian taxa might in fact represent several races of a single species. Yet in the very same year, Reischütz (1983c) classified *B. geyeri, B. noricum, B. reisalpense,* and *B. cisterciensorum* explicitly as subspecies of *B. acicula,* and *B. bormanni* became [as originally described (Stojaspal, 1978)] a subspecies of *B. tschapecki.* Besides more or less explicit biogeographic considerations, Reischütz argued primarily based on similarities, but he did not define these similarities, *i.e.* he did not provide measurements of the shells. Thus, the principles behind these classifications and their rapid changes remain unclear.

Figs. 3-7 seem to confirm Reischütz's conclusions in that *Bythiospeum elseri* and *B. geyeri* are very similar. *B. noricum* and *B.* sp. from St. Martin also come close to the former taxa. Considering only shape, we also find, in addition to the above-mentioned species, *B. pfeifferi* and *B.*

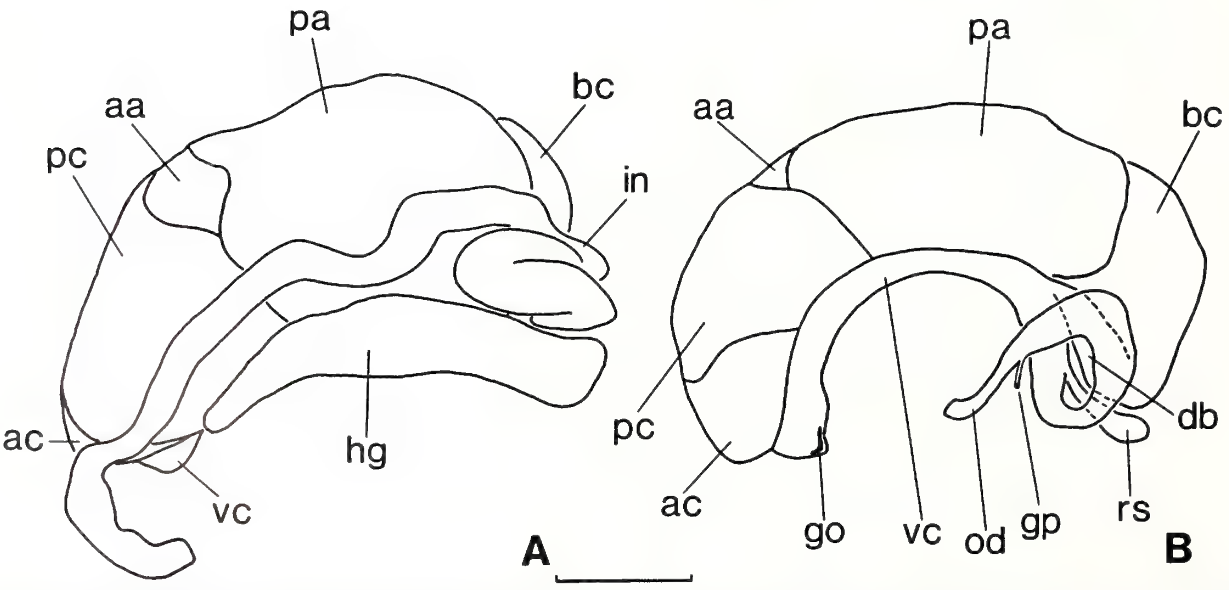

Fig. 11. *Bythiospeum* cf. *geyeri* from Vienna, mantle cavity organs (except gill and osphradium) of a female. **A.** From dorsal. **B.** From the left. (aa, anterior albumen gland; ac, anterior capsule gland; bc, bursa copulatrix; db, bursal duct; go, genital opening; gp, gonopericardial duct; hg, hypobranchial gland; in, intestine; od, oviduct; pa, posterior albumen gland; pc, posterior capsule gland; rs, receptaculum seminis; vc, ventral channel.) Scale bar = 200 µm.

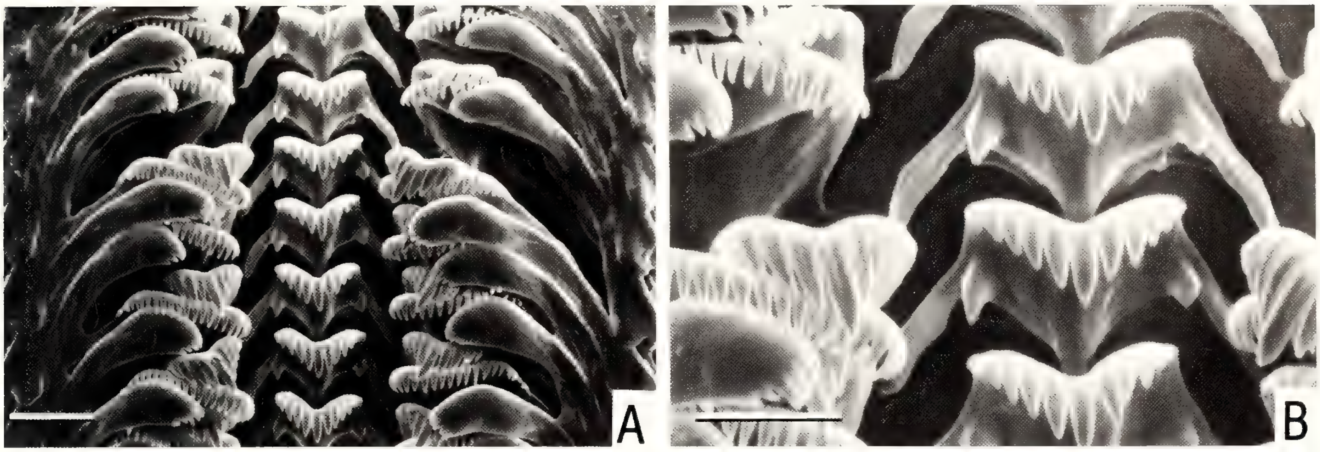

Fig. 12. *Bythiospeum* cf. *geyeri* from Vienna, radula (SEM). **A.** seven transverse rows; **B.** Rachidian teeth. Scale bars = 10 µm (A); 5 µm (B).

tschapecki in a cluster of slender species (Fig. 6). *B. cisterciensorum* and *B. reislapense*, on the other hand, can hardly be regarded as similar to *B. geyeri* (*contra* Reischütz, 1983a, c, 1988b). They are the relatively widest (sh:sw) species (Fig. 3). *B. bormanni* comes closest to them (Figs. 3-7). A relationship to *B. tschapecki* based on conchological similarity can hardly be inferred (*contra* Stojaspal, 1978; Reischütz, 1983c). *B.* sp. and *B. tschapecki* are obviously two distinct, sympatric species. Because Reischütz (1983b) did not realize that his series from St. Martin contained two species (see above), it is unclear whose anatomy he described.

The four series of or attributed to *Bythiospeum geyeri* are quite distinct in size, but relatively similar in shape (Figs. 2, 4-7). Only the alluvial sample from Schönbühel, which is almost equally distant to all other series (Table 4), does not cluster with its (presumably) conspecific populations (Figs. 4 and 6), but it has its nearest neighbor on the minimum spanning trees of Figs. 5 and 7 in *B.* cf. *geyeri* from Vienna.

Whether these four series really belong to one species can hardly be determined from these morphometric comparisons. The same holds for whether *Bythiospeum elseri* should or should not be considered synonymous with *B. geyeri*. In general, shell morphology is hardly appropriate for the analysis of relationships among hydrobiids. Because the shells are, as in the present case, mostly very simple, it is often impossible to assess whether similarities are due to common descent or to convergence. Therefore, systematic statements must be based primarily on anatomical investigations. There are also cases of sibling species, *i.e.* species with identical shell shape but distinct anatomy [*e.g. Hemistomia caledonica* Crosse, 1872, and *H. fluminis* Cockerell, 1930 (pers. obs.), or two Austrian species of *Belgrandiella* Wagner, 1928 (Haase, in prep.)], as well as cases where conspecific populations reveal significant differences [*e.g. Graziana pupula* (Westerlund, 1886) (Haase, 1994)].

For the present contribution it should be considered again that especially the alluvial samples might contain shells of more than one population or species, which would have distorted the analysis severely. Until more anatomical data are available for Austrian *Bythiospeum*, it is suggested to classify each sample as separate species. Only then is it meaningful to discuss relationships and biogeographic implications.

ECOLOGY OF *BYTHIOSPEUM* CF. *GEYERI* FROM VIENNA

Danielopol *et al.* (1992) measured parameters such as temperature, dissolved oxygen, dissolved organic carbon, and bacterial activity, in several monitoring wells around the Eberschüttwasser. Most noteworthy is the low concentration of oxygen. During more than six of nine months of continuous observation, the conditions were hypoxic with oxygen concentrations below 1 mg/l. Only in winter did the situation seem to improve. Despite this deficiency of oxygen, Pospisil (1989) found quite a rich stygofauna with a number of amphipod, cyclopoid, isopod, ostracod, and harpacticoid crustaceans, and a second hydrobiid gastropod, *Lobaunia danubialis* Haase, 1993 (Haase, 1993a).

How these animals are adapted to these hypoxic conditions is hardly understood. Danielopol *et al.* (1992) observed behavioral differences between the isopods *Proasellus slavus* (Remy, 1948) and *Asellus aquaticus* (Linné, 1758), the former a stygobiont and the latter from epigean waters, when exposed to different oxygen concentrations. *P. slavus* kept the frequency of pleopod beats constant in contrast to *A. aquaticus*. Although the high tolerance of oxygen deficiency of *P. slavus* can certainly not be explained by behavior alone, the underlying physiological

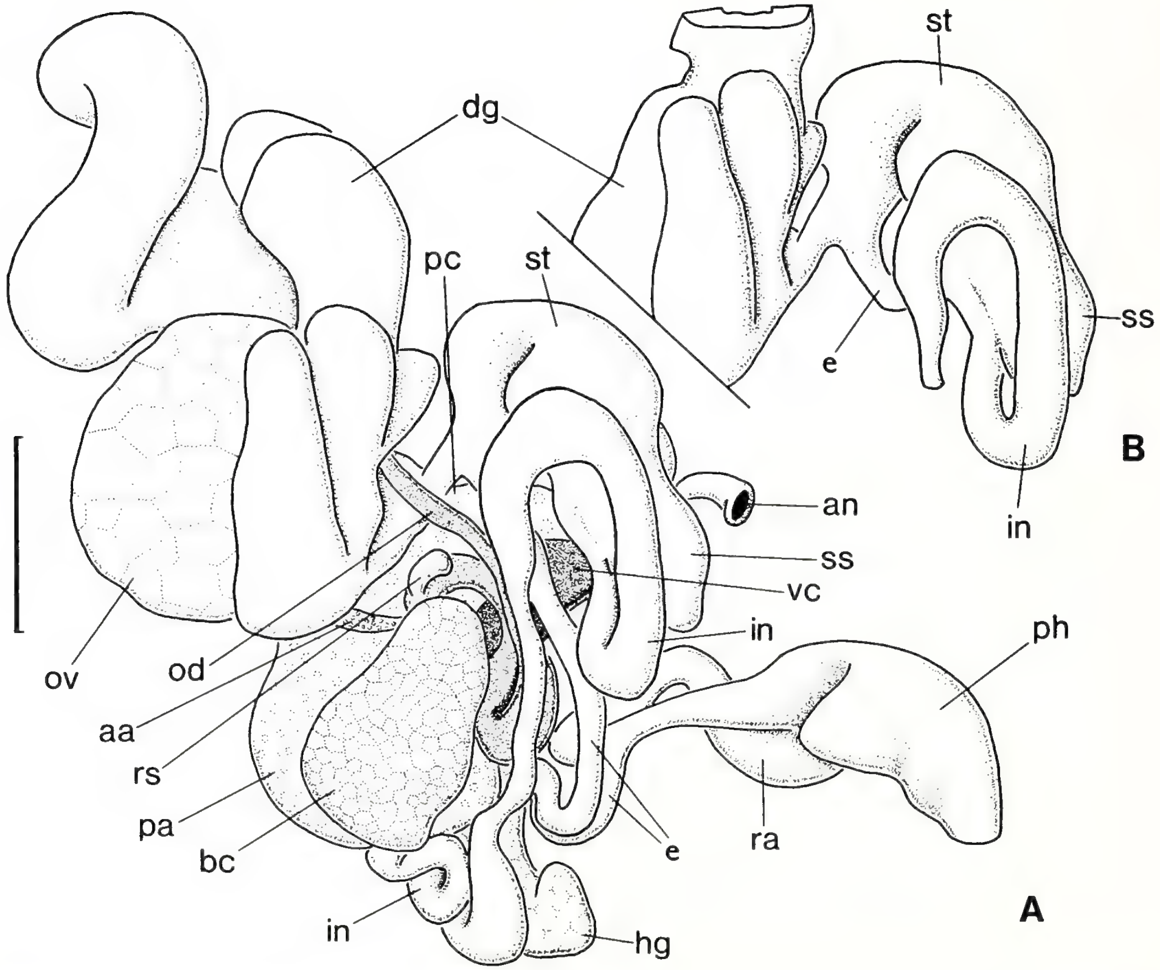

Fig. 13. *Bythiospeum* cf. *geyeri* from Vienna, genital and digestive systems (without salivary glands) of a female. **A.** Aspect from the right; different stipplings serve only for clarity and do not imply structures or colors. **B.** Section of the digestive system, slightly turned. (aa, anterior albumen gland; an, anus; bc, bursa copulatrix; dg, digestive gland; e, esophagus; hg, hypobranchial gland; in, intestine; od, oviduct; ov, ovary; pa, posterior albumen gland; pc, posterior capsule gland; ph, pharynx; ra, radula sheath; rs, receptaculum seminis; ss, style sac; st, stomach; vc, ventral channel.) Scale bar = 200 µm.

adaptations remain unclear. The adaptations of *Bythiospeum geyeri* must be primarily physiological, because the gill is definitely reduced in size and in number of filaments.

ANATOMY OF *BYTHIOSPEUM* CF. *GEYERI* FROM VIENNA

The lack of pigmentation and eyes is a consequence of the subterranean habitat of *Bythiospeum geyeri*. Seibold (1904) claimed to have found rudiments of the eye in *B. quenstedti* (Wiedersheim, 1873), but his figure is not convincing. He probably mistook a large cell for the *anlage* of an eye.

The black granules in the connective tissue around the stomach and the distal lobes of the digestive gland were also found in *Bythiospeum quenstedti* (*fide* Seibold, 1904). Their function is not known.

Bythiospeum geyeri has a number of plesiomorphic features, that is, features that are believed to be primitive within the family Hydrobiidae: the large hypobranchial gland, the rachidian tooth with only a single pair of basal cusps, the short but distinct cerebropleural connectives, the sac-shaped female and male gonads, the simple penis lacking any muscular or glandular appendages, and the duct connecting the prostate and mantle cavity.

The hypobranchial gland is often reduced in hydrobiids. In *Belgrandiella* and *Graziana*, its size can be used to diagnose species (Haase, 1994).

In many hydrobiid species cerebral and pleural ganglia are fused. The retention of a distinct connective is certainly primitive.

The forms of the rachidian tooth, the penis, and the

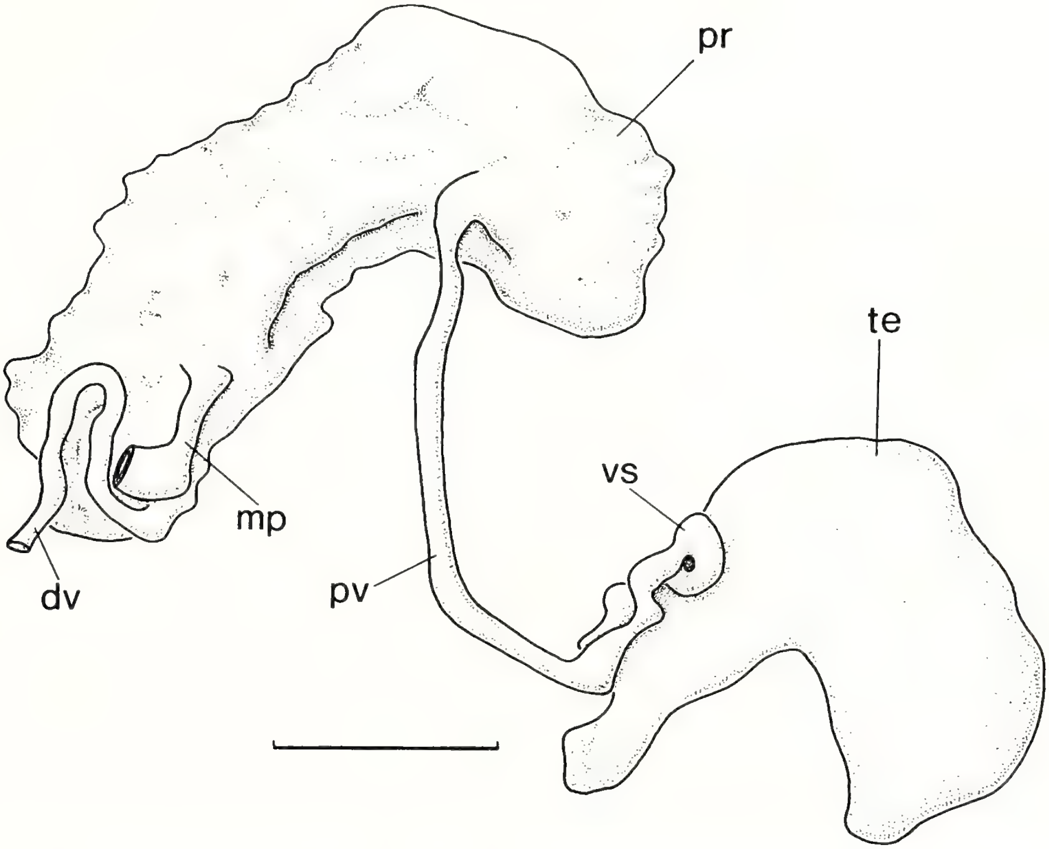

Fig. 14. *Bythiospeum* cf. *geyeri* from Vienna, genital system of a male. (dv, distal vas deferens; mp, duct connecting mantle cavity and prostate; pr, prostate; pv, posterior vas deferens; te, testis; vs, vesicula seminalis.) Scale bar = 200 µm.

gonads are believed to be primarily simple and not reduced (as to the gonads *contra* Davis, 1980).

The prostatic duct opening into the mantle cavity has not been reported for any other species of the genus *Bythiospeum*. In dissections it is hardly detectable, but Seibold (1904) and Krull (1935), who also made histological serial sections of *B. quenstedti*, did not mention it either. But it is present in *Hydrobia* Hartmann, 1821 (Johansson, 1948; Haase, 1993b) and *Heleobia dobrogica* (Negrea and Grossu, 1989) (pers. obs.). From an evolutionary point of view this duct represents the incomplete closure of the open, pallial, prostatic groove found in basal caenogastropods (Fretter and Graham, 1962; Ponder, 1985, 1988). According to Fretter and Graham (1962) this duct might have a compensatory function for the rapid retraction of the male in case of disturbance during copulation.

Whether the peculiar formation of the connective tissue surrounding the stomach and digestive gland, the position of stomach and digestive gland, and their connection through a duct, represent ancestral states or autapomorphies cannot be judged at present.

There is anatomical information on a number of species of the genus *Bythiospeum* (Seibold, 1904; Krull, 1935; Bole, 1970; Boeters, 1971, 1984a, b; Giusti and Pezzoli, 1980; Radoman, 1983; Reischütz, 1983b, 1988a; Bernasconi, 1990). Unfortunately, many of these descriptions are incomplete or do not depict the organs in their natural positions, which is probably due to the small number of specimens available in most cases, and because most of these authors did not have the opportunity to prepare histological serial sections. Thus, comprehensive comparisons are hardly possible at present. It can only be concluded that practically all organs are potentially important for differential diagnoses. In addition, this is only a very small fraction of the nominal species described in this genus so that we are far from tracing the evolution of and establishing relationships among *Bythiospeum* species.

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HPLC analysis of chloroplast pigments from the marine ascoglossan *Tridachia crispata* (Mörch, 1863) (Mollusca: Opisthobranchia)

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Abstract. Pigment composition of ingested kleptoplastids (= "symbiotic chloroplasts"; Waugh and Clark, 1986) in the marine ascoglossan *Tridachia crispata* (Mörch, 1863) were analyzed for the first time using reverse-phase high performance liquid chromatography (HPLC). The pigment signatures from the slug closely reflected that of the host plant *Caulerpa sertularioides* (Gmelin). One noted exception was the detected presence of fucoxanthin in the tissues of *T. crispata* which is attributed to the ingestion of epibenthic microflora (diatoms) from the surface of the host plant. This demonstrates for the first time that plant pigments in the tissues of *T. crispata* are not exclusively from the host plant. Additionally, the detection of phaeophorbide-a and phaeophytin-a (chlorophyll-a decay products) in *T. crispata* suggested that there was some minor breakdown (via digestion) of pigment during the transfer.

Tridachia crispata (Mörch, 1863) is a marine ascoglossan (= sacoglossan) which feeds on several species of Siphonales algae including *Caulerpa sertularioides* (Gmelin). The slug ingests intact chloroplasts from the alga and retains them in its digestive diverticula. The chloroplasts apparently retain the ability to undergo photosynthesis and provide nutrients to *T. crispata* during periods of food scarcity (Hinde and Smith, 1974; Waugh and Clark, 1986). Several opisthobranch species are capable of surviving 14-70 days without external nutrients (Hinde and Smith, 1974; Taylor, 1970a, b; Keefer, pers. comm.).

The degradation products of chloropigments, commonly referred to as phaeopigments, have been used to infer the availability of different source materials to consumers. For example, the three dominant tetrapyrrole derivatives of chloropigments (phaeophorbide, phaeophytin, and chlorophyllide) are typically formed during bacterial, autolytic cell lysis, and metazoan grazing activities (Sanger and Gorham, 1970; Shuman and Lorenzen, 1975; Hawkins *et al.*, 1986; Bianchi *et al.*, 1988, 1991). Differences in the production of phaeophorbide during grazing activity has been shown to be reflective of the quality of food resources (Shuman and Lorenzen, 1975; Bianchi *et al.*, 1988, 1991). Thus, higher quality food resources will result in the production of greater amounts of phaeophorbide.

Previous studies on symbionic chloroplasts (*i.e.* "kleptoplastids," Waugh and Clark, 1986) associated with several species of Ascoglossa have dealt primarily with descriptions of these phenomena, as well as carbon translocation, physiological measurements of oxygen production, and photosynthetic rates (Hinde and Smith, 1974; Taylor, 1967, 1968, 1970a, b; Trench, 1969, 1980; Trench *et al.*, 1969). To date, no studies have been published on the quantitative measurement of chlorophylls and carotenoids of intact symbionic chloroplasts in opisthobranchs using "state-of-the-art" HPLC.

The objectives of the present study were to: (1) quantitatively measure, using reverse-phase high performance liquid chromatography (HPLC), pigment concentrations in chloroplasts from intact specimens of *Caulerpa sertularioides* and from chloroplasts ingested by adult *Tridachia crispata*; and (2) determine if any observable differences exist between the pigment content of intact algae and that of chloroplasts from the digestive diverticula of the slug.

MATERIALS AND METHODS

COLLECTION AND MAINTENANCE

Adult *Tridachia crispata* (> 25 mm length) and samples of *Caulerpa sertularioides* were collected at Key Largo, Florida, U. S. A., during March 1994. The specimens were maintained on a 12:12 light/dark photoperiod in glass containers (1000 ml) containing aerated Instant Ocean® artificial seawater (32 ppt salinity and 18° ±

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0.5°C). The water in each container was replaced daily with fresh seawater. The slugs were fed *C. sertularioides* for 2 wk prior to HPLC analysis. After 2 wk, individual *T. crispata* and *C. sertularioides* fronds were removed from the apparatus, rinsed with filtered (0.22 µm) seawater, blotted dry, and immediately frozen (-80°C) for HPLC analysis.

PLANT PIGMENT EXTRACTION AND ANALYSIS

Frozen plant and animal tissues were lyophilized, weighed, and extracted for pigments using 100% acetone according to Bianchi *et al.* (1993). Tissue samples were frozen immediately (-80°C) to prevent the possibility of post-mortem phaeopigment production in the guts of the animals (Millie *et al.*, 1993). Lyophilization of plant and animal tissues for pigment extractions has been shown to be the preferred method for quantification (Millie *et al.*, 1993). To preclude any artifacts from light effects, all extractions were performed under low light conditions, however, methods using methanol tend to be more problematic (Bianchi *et al.*, 1995). The formation of phaeopigments in acetone extracts using the method described in Bianchi *et al.* (1993) has been shown to be minimal. Canthaxanthin was added to each of the acetone extracts as an internal standard to confirm that there was no loss of pigments during extraction.

Reverse-phase HPLC analysis was conducted using the method of Wright *et al.* (1991); the gradient used in this method has recently been described as the selected method for pigment analyses (Millie *et al.*, 1993). A Waters® Model 660 solvent-delivery system was coupled with dual-channel detection using a Waters® Model 990 photodiode array detector set at 438 nm for absorbance, and a Milton-Roy® fluorescence detector with excitation set at 440 nm and emission at > 600 nm. The injector was connected via a guard column to a reverse-phase C_{18} Alltech® Adsorbosphere column (5 µm particle size; 250 mm x 4.6 mm i.d.). After injection (100 µl), a gradient program (1 ml/min) began isocratically at time zero with mobile phase A (80:20 methanol: 0.5 M ammonium acetate, aq.; pH 7.2 v/v) which then ramped to 100% mobile phase B in 4 min (90:10 acetonitrile : HPLC grade water v/v) and then changed to 20% B and 80% mobile phase C (100% ethyl acetate) in 35 min. This was followed by a return to 100% B in 3 min with final ramping to 100% A in 3 min. This method provided sufficient resolution of all pigments of interest in *Tridachia crispata* and *Caulerpa sertularioides* (Figs. 1, 2). Although fluorescent chromatograms are not presented here, a fluorescence detector was used as a simple means of identifying chloropigments versus carotenoids.

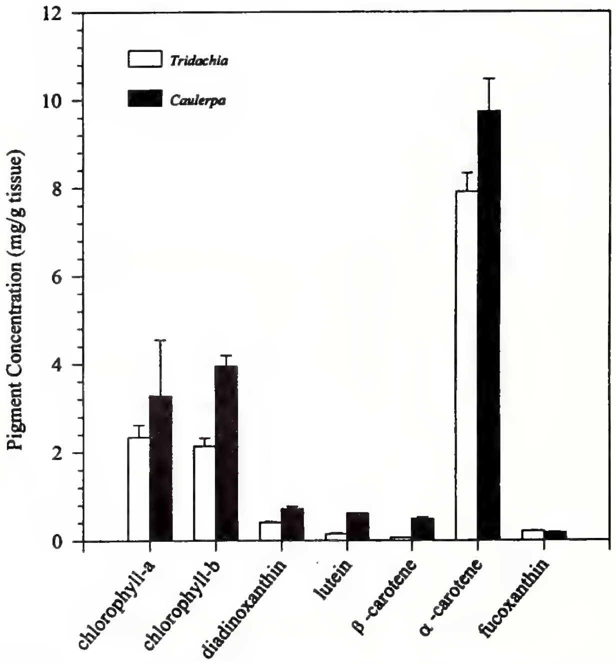

Fig. 1. Dominant pigment concentrations (mg/g tissue; mean ± S.E.) found in tissues of *Tridachia crispata* and *Caulerpa sertularioides*.

High purity HPLC standards for chlorophylls a and b as well as α and β carotene were obtained from Sigma Chemical Co. (St. Louis, Missouri). Standards of the following carotenoids were kindly provided by Hoffman LaRoche Co. (Basil, Switzerland): fucoxanthin, diadinoxanthin, lutein. All standards were spectrophotometrically verified for purity. Peak identifications were based on retention times of standards and confirmed with a diode-array detector. All peaks were quantified with calculated response factors and the Water Millenium software package (Waters Corporation, Inc.; Bianchi *et al.* 1995).

Pigment concentrations of *Tridachia crispata* and *Caulerpa sertularioides* tissue were tested for comparison using Pearson's Product-Moment Correlation Coefficient (Sokal and Rohlf, 1981). A probability level of < 0.001 was considered significant for statistical analysis.

RESULTS AND DISCUSSION

There was a strong correlation (Pearson's Product-Moment Correlation Coefficient; P < 0.001) in the occurrence of dominant plant pigments (carotenoids and chlorophylls) in *Tridachia crispata* and *Caulerpa sertularioides* (Fig. 1). The only pigments found exclusively in *T. crispata* were phaeophorbide-a and phaeophytin-a (labelled as peaks 11 and 12 in the *T. crispata* chromatogram; Fig. 2A). All pigment concentrations/g tissue were significantly higher (P < 0.001) in *C. sertularioides* than in *T. crispata*. The

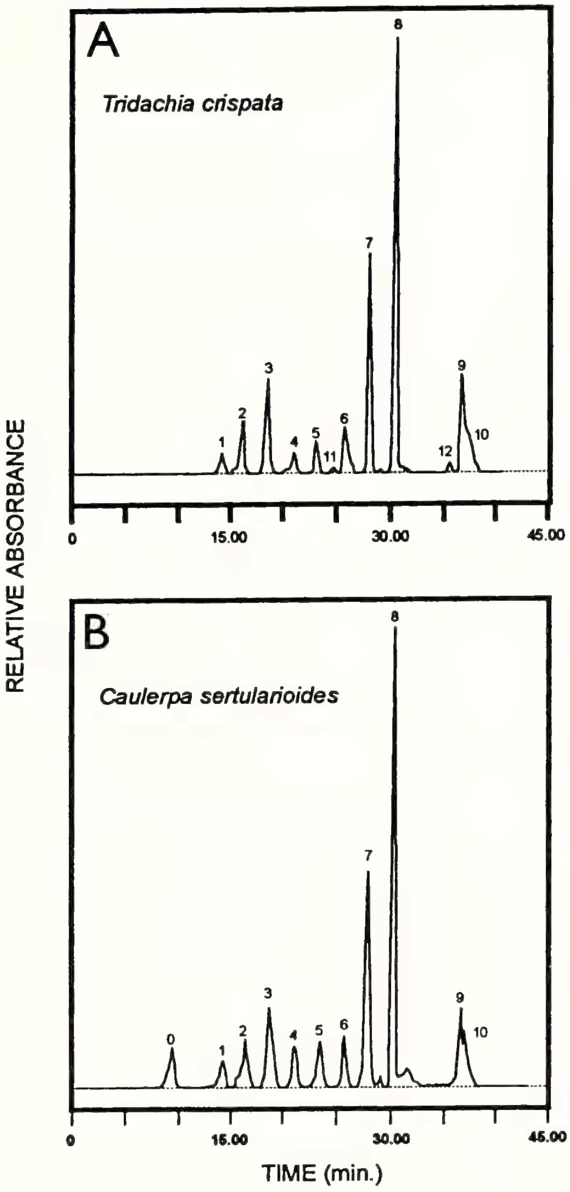

Fig. 2. Absorbance chromatograms showing plant pigments extracted from the tissues of: **A.** *Tridachia crispata*, and **B.** *Caulerpa sertularioides*. Identified pigments are: 0 = chlorophyll-c; 1 = siphonaxanthin; 2 = fucoxanthin; 3 = 9-cis-neoxanthin; 4 = violaxanthin; 5 = diadinoxanthin; 6 = lutein; 7 = chlorophyll-b; 8 = chlorophyll-a; 9 = ∝-carotene; 10 = β-carotene; 11 = phaeophorbide-a; 12 = phaeophytin-a.

removal and translocation of chloroplasts, from *C. sertularioides* to *T. crispata* tissue, occurred with minimal pigment loss.

The presence of phaeophorbide-a and phaeophytin-a in *Tridachia crispata* was due to moderate breakdown (via digestion) during the transfer of pigments. Phaeophorbide is a chlorophyll decay product typically produced by heterotrophic grazing processes (Shuman and Lorenzen, 1975; Bianchi *et al.*, 1988). Moreover, the presence of fucoxanthin and chlorophyll-c (pigment markers for diatoms) in *Caulerpa sertularioides* extracts (Fig. 2B) provides evidence that epibenthic microflora were present, and primarily composed of diatoms. Fucoxanthin, not normally found in Chlorophyta, such as *C. sertularioides*, was also found in *T. crispata* (Fig. 2A). Although we did not use epiphyte-free algae (Fig. 3), we are confident that the fucoxanthin found in the *C. sertularioides* was from an external source; this is based on the extensive literature of pigments in algae (Rowan, 1989) as well as microscopical evidence of diatoms in the culture water of *C. sertularioides* (Fig. 3). This suggested that chloroplasts from epibenthic microflora on the surfaces of algae consumed by *T. crispata* were also transported into their tissues. It was previously thought that only robust chloroplasts of the Siphonales algae contributed to the pigment signature of *T. crispata* tissue (Giles and Sarafis, 1972), and the majority of the pigment signatures support this belief. However, the presence of fucoxanthin suggested that intact chloroplasts from other sources (*i.e.* epibenthic diatoms) are likely to have been ingested while the slug was feeding on *C. sertularioides*. Selective feeding on diatoms has been previously documented in *Elysia evelinae* Marcus, 1957 (Jensen, 1981); however, in the present study we did not directly observe preferential feeding on epibenthic diatoms by *T. crispata*. It is improbable that the fucoxanthin may have arisen from other sources though, because this pigment decays rapidly once outside of the thylakoid membrane (Bianchi *et al.*, 1991). The conventional spectrophotometric and fluorometric methods previously used for examining plant pigments in *T. crispata* would not detect these subtle differences in pigment signatures.

While chloroplasts have been shown to be capable of providing resources to *Tridachia crispata* via photosynthate production, they could also prove to be important in shielding these animals from the deleterious effects of UV irradiation. Carotenoids, such as zeaxanthin and β-carotene, function as photoprotectants for living plants, by quenching singlet oxygen which precludes peroxidation reactions (Foote *et al.*, 1970). Thus, the abundance and distribution of photoprotectants (such as pigments) in organisms may prove to be very important with the current global trends in stratospheric ozone depletion (via enhanced UV-B). However, before any specific claims can be made concerning the photoprotectant nature of these pigments further work is needed to determine the overall abundance and distribution of pigments in the tissues of the organism.

CONCLUSIONS

In this study, we have examined for the first time (using state-of-the-art HPLC) differences in the concentration and composition of plant pigments in chloroplasts

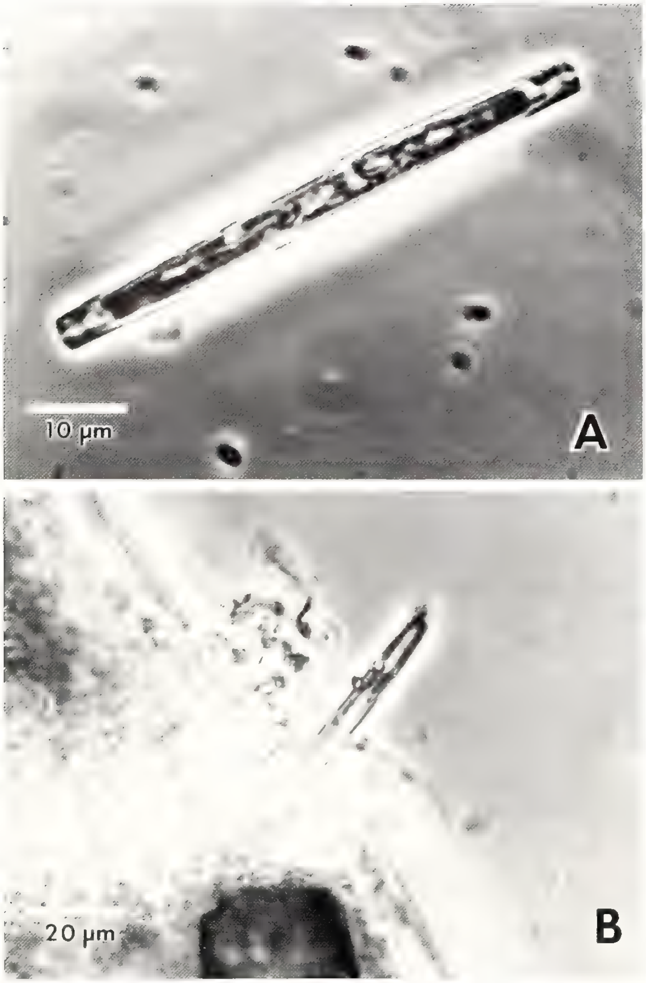

Fig. 3. A. Phase-contrast micrograph of pennate diatom in culture water of *Caulerpa sertularioides*. **B.** Phase-contrast micrograph of pennate diatom adhering (via cellular debris) to frond of *C. sertularioides*.

located in *Tridachia crispata* and the source plant itself (*Caulerpa sertularioides*). We have also demonstrated the probable ingestion of epibenthic diatoms by *T. crispata*, indicated by the presence of fucoxanthin in the slug's tissues. Thus, the pigment composition in the slug is not exclusively derived from the Siphonales algae. This study and others (see review of Millie *et al.*, 1993) illustrate the utility of HPLC analysis in trophic studies of benthic marine invertebrates.

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Population ecology of the endangered Ouachita rock-pocketbook mussel, *Arkansia wheeleri* (Bivalvia: Unionidae), in the Kiamichi River, Oklahoma

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Abstract. The only known remaining viable population of *Arkansia wheeleri* Ortmann and Walker, 1912, in the world occurs within a 128-km stretch of the Kiamichi River in Pushmataha County, Oklahoma. Within this river, *A. wheeleri* occurs only within the most species-rich mussel beds. In its optimal habitat, this species is always rare; mean relative abundance varies from 0.2-0.7% and the mean density is 0.27 individuals/m^2. The youngest individual *A. wheeleri* encountered was approximately 12 years of age. Forty-three percent of the historically known subpopulations of *A. wheeleri* below where inflow from an impounded tributary enters the Kiamichi River have apparently been extirpated, and no new subpopulations have been located. *A. wheeleri* survives at 75% of the historically known locations above the impounded tributary and five new subpopulations have been located.

Arkansia (syn. *Arcidens*) *wheeleri* Ortmann and Walker, 1912 (Bivalvia: Unionoidea), the Ouachita rock-pocketbook mussel, is a federal endangered species (Federal Register, 1991). Originally named *Arkansia wheeleri* by Ortmann and Walker (1912), Clarke (1981, 1985) recognized *Arkansia* as a subgenus of *Arcidens*. The species was considered by Clarke to be distinct. However, Turgeon *et al.* (1988) have continued to use the binomial *Arkansia wheeleri.*

The historical distribution of *Arkansia wheeleri* was in the Ouachita and Little Rivers in Arkansas and the Kiamichi River in Oklahoma, all south-flowing rivers out of the Ouachita Mountains (Fig. 1). A survey by Clarke (1987) indicated that the species was probably extirpated from the Ouachita River and severely depleted in the Little River in Arkansas. In 1992 and 1993, relict shells of *A. wheeleri* were found in the Little River in Oklahoma below Pine Creek Reservoir (Vaughn, 1993).

Arkansia wheeleri was first reported from the Kiamichi River by Isely (1924) who conducted a survey of the river in 1911. Clarke (1987) and Mehlhop and Miller (1989) both conducted recent status surveys for this species in the Kiamichi River. They found that *A. wheeleri* was patchily distributed and rare in the Kiamichi River from above Hugo Reservoir to Whitesboro (Fig. 2). Since the construction of a dam and reservoir in the lower reaches of the Kiamichi in the 1970s, some of the backwater areas where it was known to occur have been destroyed (Valentine and Stansbery, 1971), and connection with potential habitats on the Red River and other tributaries to it has been blocked. Based on the above information *A. wheeleri* was listed as endangered in October 1991 (Federal Register, 1991).

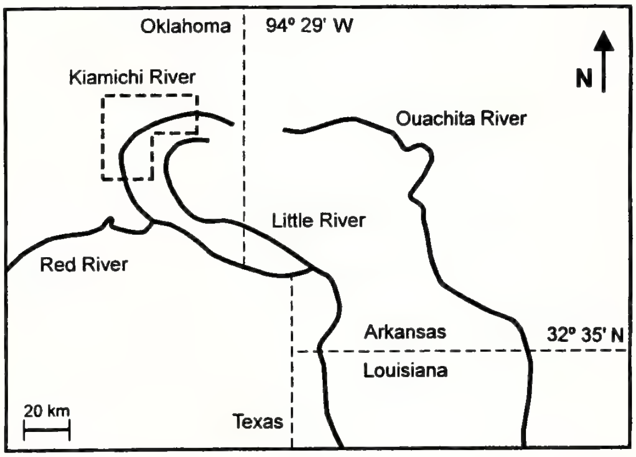

Fig. 1. Rivers in which *Arkansia wheeleri* historically occurred. Dashed box indicates area depicted in Fig. 2.

The objectives of this study were to determine the distribution and abundance of *Arkansia wheeleri* in the Kiamichi River, characterize the species' microhabitat, and determine movement, growth, and survivorship of individuals. We also examined the impact of a reservoir on the population.

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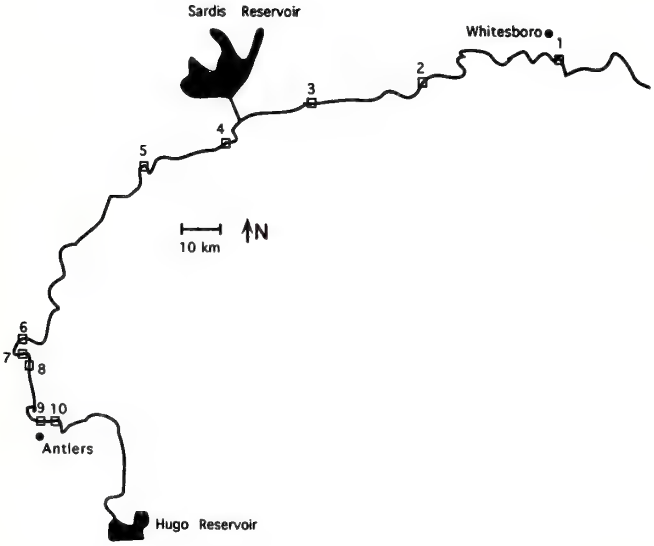

Fig. 2. Population monitoring sites for *Arkansia wheeleri* on the Kiamichi River.

STUDY SITE

The Kiamichi River is a major tributary of the Red River. It flows for a total of 180 km through a 4,800 km^2 drainage area across the Ridge and Valley Belt of the Ouachita Mountain geologic province and the Dissected Coastal Plain province (Curtis and Ham, 1972). The average gradient of the river is 0.47 m/km. Two reservoirs influence the river: Sardis Reservoir is an impoundment of Jackfork Creek, a tributary of the Kiamichi River. Hugo Reservoir is an impoundment of the lower Kiamichi River. The vegetation cover in the watershed can be described as a patchwork of forest made up of short-leaf and loblolly pine, mesic oak forests, and diverse bottomland habitats in various stages of maturity. Another large component of the watershed coverage is made up of pasture and other agricultural lands (Vaughn *et al.*, 1993).

The Kiamichi River is located near the western edge of mussel species richness in the United States (Williams *et al.*, 1992; Warren and Burr, 1994). Therefore, because of historical biogeographic factors, one would not expect diversity in the Kiamichi River to be as high as that in rivers in more eastern states. Nevertheless, the Kiamichi River has high mussel diversity for its size and geographic location. Fifty-five species of mussels are known from Oklahoma (Williams *et al.*, 1992), and 29 of these currently occur in the Kiamichi River (Vaughn *et al.*, 1993). Only two species that were known historically from the Kiamichi River (Isley, 1924) no longer occur there. Several species of mussels from the Kiamichi River are endemic to rivers in the Ouachita Mountains, including *Arkansia wheeleri*, *Ptychobranchus occidentalis* (Conrad, 1836) and *Villosa arkansasensis* (Lea, 1862) (Pyron and Vaughn, 1994). *P. occidentalis*, the Ouachita kidneyshell, is a candidate for federal listing.

METHODS

Our quantitative survey efforts were restricted to areas that contained concentrations of mussels and thus could be defined as "beds." Mussel relative abundance and habitat data for 22 sites in the Kiamichi River were collected during July-August 1990. These sites included 11 areas defined as "pools," six areas defined as "backwaters," and five areas defined as "runs" (see Discussion). Mussel surveys (timed to standardize sampling effort) (Green *et al.*, 1985; Kovalak *et al.*, 1986) were conducted by hand-searching with the aid of SCUBA in deeper areas and by hand searches in shallow areas in the following manner: (1) a shoal was identified for surveying; (2) the entire area was searched by at least two people for one hr; (3) all mussels encountered were removed to shore; (4) all mussels were immediately identified; (5) mussels were put back into the water as close to where they were removed as possible.

At each of the 22 sites, we measured water depth, water temperature, current velocity, conductivity, dissolved oxygen, and pH. Five measures of water depth and current velocity were taken across the mussel bed and averaged. Current velocity was measured 10 cm above the stream bottom with a Marsh-McBirney model 201 portable flow meter. Conductivity and dissolved oxygen were measured with Yellow Springs Instruments conductivity and dissolved oxygen meters, respectively. pH was measured with a Fisher Accumet portable pH meter.

At each site, we recorded the proximity of the site to entering tributaries, islands, and macrophyte cover. Three replicate substratum samples were collected at each site. These were brought back to the laboratory and allowed to dry. Samples were dry sieved, weighed, and individual proportions of samples were assigned to the appropriate substratum size class (in mm) following Hynes (1970:24). Standard sieving techniques do not segregate particles greater than about 2 mm in diameter (*i.e.* gravel from pebble from cobble). To determine the proportion of fine gravel, coarse gravel, pebble, and cobble in samples we randomly measured the diameter of 100 particles in the subsample greater than 2 mm in particle diameter (Dunne and Leopold, 1978).

In 1991, we selected ten of the 22 sites as long-term population monitoring sites for *Arkansia wheeleri* (Fig. 2). The ten sites were chosen to be as evenly distributed as possible along the Kiamichi River above Hugo Reservoir, but still be reasonably accessible, and included sites where *A. wheeleri* had been located by us in 1990, sites where it had been found historically (Mehlhop and Miller,1989; Clarke, 1987), and sites above and below the Sardis Reservoir and Jackfork Creek. Density and relative abundance data for mussel species at the ten monitoring sites were collected during July-August 1991. Densities were calculated from quadrat samples and relative abundances were estimated from timed searches, as described above. Quadrat sampling was done with quarter-meter-square PVC pipe quadrats. Fifteen random quadrats were sampled for each site. Quadrats were searched by hand, with the aid of SCUBA in deeper areas, until all mussels had been recovered to a depth of 15 cm. Individual mussels were returned to the mussel bed as in timed searches. All *A. wheeleri* were measured using digital calipers (height, width, and length), and individually marked using numbered, laminated plastic fish tags. All specimens were returned to the same location from which they were captured.

To obtain additional information on *Arkansia wheeleri* size and age distribution, we measured relict shells of *A. wheeleri* deposited in the Oklahoma Museum of Natural History (OMNH, University of Oklahoma, Norman) or that we found on the Kiamichi River between 1990 and 1992. We counted external annuli on shells we had collected and those in OMNH (Neves and Moyer, 1988; McMahon, 1991). From the above data, we calculated shell length, width, and height vs. number of annuli regression lines. Shell height vs. number of annuli produced the best fit, and the resulting equation was used to predict the number of annuli for live mussels that had been measured in the field. We used Replicated Goodness of Fit tests (G_H) (Sokal and Rohlf, 1981) to compare size distributions of relict shells and live mussels, and to compare predicted age distributions of mussels.

We used several statistical techniques to explore relationships between *Arkansia wheeleri* distribution and abundance and measured habitat parameters. For all of these analyses, we used the data collected from the 22 sites in 1990. Associations between *A. wheeleri* and other species of mussels were calculated using Spearman Rank correlations on relative abundance data (Ludwig and Reynolds, 1988). We used discriminant function analysis (Sokal and Rohlf, 1981) to predict the presence or absence of *A. wheeleri* at a site based on the habitat characteristics of that site. We used an independent-sample t-test (one-tailed) (Sokal and Rohlf, 1981) to compare species richness at sites with and without *A. wheeleri.*

RESULTS

Arkansia wheeleri was found in ten of the 22 mussel beds that were sampled. Six of these ten sites were classified as pools and four were classified as backwaters. No specimens were found in any of the run areas sampled. A multivariate analysis of variance using all of the habitat variables to predict the presence or absence of *A. wheeleri* at a site was not significant ($F_{(12,9)} = 1.22$, $P = 0.39$). A significant discriminant model was produced using four habitat variables: depth, habitat type (pool, backwater, or run), presence or absence of emergent vegetation at the site, and mussel species richness (Table 1). This model successfully predicted the presence or absence of *A. wheeleri* 17 out of 22 times ($G_{(1)} = 7.72$, $P = 0.005$). Mussel species richness at a site was the best individual predictor of *A. wheeleri* occurrence (Table 1). Mussel sites where *A. wheeleri* occurred were more species-rich than other mussel sites that we sampled in the Kiamichi River ($t_{(15)} = 3.18$, $P = 0.006$).

Table 1. Results of univariate F-tests of the presence or absence of *Arkansia wheeleri* at a site using four habitat variables. The multivariate model is significant ($F_{(1,20)} = 0.54$, $P = 0.03$).

Variable	$F_{(4,17)}$	P
Depth	6.87	0.016
Habitat type (pool, backwater, or run)	0.95	0.342
Emergent vegetation (presence/absence)	5.45	0.030
Mussel species richness	10.72	0.004

Spearman rank correlations of relative abundance data revealed three significant associations between *Arkansia wheeleri* and other mussel species. *A. wheeleri* was positively correlated with the relative abundance of *Quadrula* cf. *apiculata* (Say, 1829) ($r_s = 0.437$, $P < 0.05$) and *Megalonaias nervosa* (Rafinesque, 1820) ($r_s = 0.423$, $P < 0.05$), and negatively correlated with *Lampsilis teres* (Rafinesque, 1820) ($r_s = -0.368$, $P < 0.05$).

In most cases *Arkansia wheeleri* was located only through timed searches and did not occur in quadrat samples. Mean relative abundance of *A. wheeleri* at monitoring sites in 1990-1992 is shown in Fig. 3 and varied from 0.2-0.7%. In 1991, *A. wheeleri* was found in quadrat samples at sites 6 and 7. This allowed us to estimate the density of *A. wheeleri* at 0.27 individuals m^2, at each of these sites.

In 1990 and 1991, we marked and released nine *Arkansia wheeleri* at the point of capture. In 1991, we recaptured only two marked individuals, although we found nine live individuals. Both recaptured specimens were found at site 3 (Fig. 2). Both of these individuals were found within one meter of where they were released in 1990. No other live *A. wheeleri* were found at site 3. In 1992, we recaptured the same two *A. wheeleri* at site 3 that we had recaptured in 1991. The individuals were within a few meters of where they had been released in 1991. The recaptured individuals had not grown discernably (*i.e.* not more than 1 mm, within the margin of error of our calipers). No other marked specimens were recaptured in 1992. The

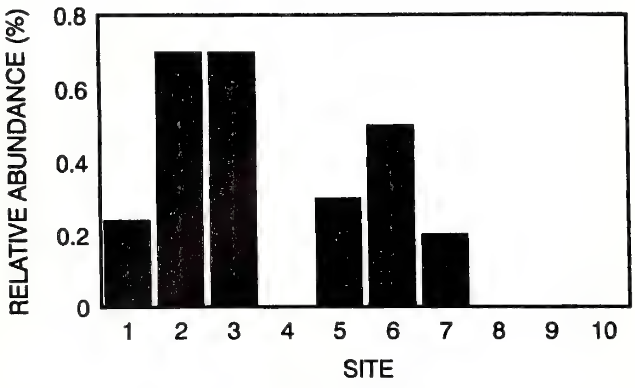

Fig. 3. Mean relative abundance of *Arkansia wheeleri* at the 10 monitoring sites in 1990-1992.

size distribution (means for 1990-1992) for *A. wheeleri* in the Kiamichi River is shown in Fig. 4.

The overall size distribution of relict shells in OMNH ($N = 50$) was significantly different than the size distribution of live *Arkansia wheeleri* in the Kiamichi River ($N = 43$) (Fig. 4, $G_{H(5)} = 23.1$, $P < 0.001$). The resulting regression equation for number of annuli on shell height was $Y = (-0.483)X + 49.62$ ($N = 24$, $R^2 = 0.467$, $P < 0.05$). We used the above equation to predict the age of *A. wheeleri* specimens from shell height. Predicted age distributions of spent shells vs. live *A. wheeleri* were also significantly different ($G_{H(12)} = 57.43$, $P < 0.001$). Using this technique, the youngest predicted age for a live specimen was 12 years. If this estimate is accurate, none of the *A. wheeleri* we encountered on the Kiamichi River during our study were produced after Sardis Reservoir was filled in 1983.

Arkansia wheeleri occurs both above and below the inflow to the Kiamichi River from Sardis Reservoir via Jackfork Creek. Of our ten monitoring sites, three were located above Sardis Reservoir and seven below (Fig. 2). All of these sites historically harbored *A. wheeleri*. *A. wheeleri* was found during this study at all three sites (100%) above Sardis Reservoir. *A. wheeleri* was found at three of seven sites (43%) below the reservoir inflow. The relative abundance of *A. wheeleri* at sites above Sardis Reservoir was generally greater than the relative abundance of *A. wheeleri* at sites below the reservoir (Fig. 3), although these differences were not statistically significant.

DISCUSSION

Prior to this study, the habitat of *Arkansia wheeleri* was reported to be backwater reaches of rivers where current is slow and where there are relatively non-shifting deposits of silt/mud and sand (Wheeler, 1918; Isely, 1924; Clarke, 1987). We found that this species occured in both pools and backwaters in the Kiamichi River, not just in backwaters as was previously believed. The distribution of *A. wheeleri* may have been underestimated in past surveys because backwaters are relatively easy to survey, whereas pools often require SCUBA.

Although pools and backwaters were considered different habitat types in this study, in reality they are tightly interconnected and share many characteristics in common. Backwater areas tend to be shallower and have finer substrata. As backwaters merge into the main river channel they turn into deeper pools with coarser substrata and slightly higher current velocities. In the Kiamichi River, *Arkansia wheeleri* occurs in both of these habitats. In addition, we believe *A. wheeleri* moves back and forth between these habitats either voluntarily or through physical displacement of shifting sediments. Locomotory tendencies differ among different mussel species. For example, individuals of *Anodonta grandis* Say, 1829, migrate up and down with changes in water level (White, 1979) and in this way avoid stranding at low water. Other species such as *Uniomerus tetralasmus* (Say, 1831) and the introduced *Corbicula fluminea* (Müller, 1774) remain in position and suffer prolonged exposure to air (McMahon, 1991). Marked individual *A. wheeleri* in a backwater area (site 3) did not move significantly from July 1990 to July 1992. However at another site (site 5), unmarked individuals moved from a backwater area into the adjacent pool area. This movement was probably the result of physical displacement of these individuals through sediment scour and redeposition.

Unlike previous surveys (Wheeler, 1918; Isely, 1924; Clarke, 1987), we did not find *Arkansia wheeleri* to be restricted to areas where the substratum was predominantly mud or fine sand. In the Kiamichi River, *A. wheeleri* is just as prevalent in gravel/cobble/coarse sand substrata (which predominates in pools) as in finer substrata. Recent studies

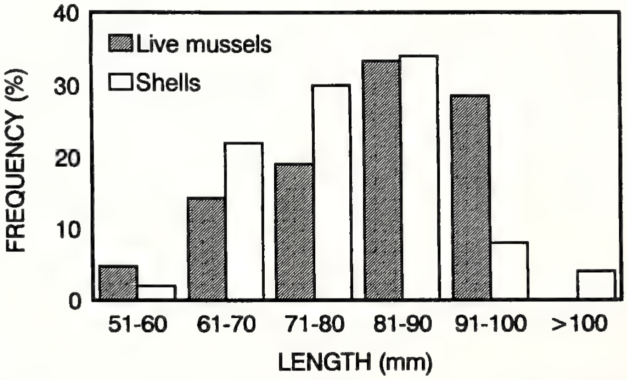

Fig. 4. Total lengths of live *Arkansia wheeleri* (N = 43) compared to relict shells (N = 50) from the Kiamichi River.

addressing the substratum preferences of unionids have reached different conclusions, and substratum preferences among unionids remain poorly understood. However, mussels are generally believed to be most successful in stable, sand/gravel mixtures and are generally absent from substrata with heavy silt loads (Salmon and Green, 1983; Stern, 1983; Cooper, 1984; Way *et al.*, 1990). Most unionid species can be found on a number of different substrata, but growth rates of individuals in each microhabitat can be quite different (Kat, 1982; Hinch *et al.*, 1989). Furthermore, many mussel species can occupy a wide range of habitats as a result of extensive larval dispersal over a heterogenous stream environment (Strayer, 1981), but growth and reproduction can be optimized only under the habitat conditions described above.

Arkansia wheeleri only occurred at the most species-rich sites in the Kiamichi River. These shoals represent optimal habitat for most mussel species, as evidenced by the large number of species and their high abundance. These shoals usually contain both pool and backwater areas, have significant gravel-bar development with accompanying vegetation [dominated by *Justicia americana* (Linné) Vahl], and are close to a tributary (usually within 0.4 km). Shoals are usually adjacent to a major riffle area, although they can be either up- or downstream of the riffle. Other studies have shown that these mainstream river shoals in shallower areas with slow, steady current and vegetation and coarse substrate are optimal habitat for lotic unionids because of minimal turbulence, low silt and steady food supply (Salmon and Green, 1983).

In the majority of mussel species, the greatest amount of growth occurs in the first few years of life. Shell growth rate then declines exponentially with age, although the rate of tissue biomass accumulation usually remains constant (McMahon, 1991). Our examination of live *Arkansia wheeleri* in the Kiamichi River and of relict *A. wheeleri* shells in museum collections indicates that this growth pattern is also followed by *A. wheeleri*. Early annuli (those near the umbo) are much wider than later annuli near the edge of the shell. Therefore, our finding of no discernable growth in the two marked individuals that we recaptured is not surprising because they were older, adult specimens.

Recruitment, growth and survival of mussels can be assessed by monitoring changes in density and size demography of natural populations (Payne and Miller, 1989). We have no quantitative historical data on densities of *Arkansia wheeleri* in the Kiamichi River or anywhere else. Past size distribution, however, can be assessed by examining the size distribution of relict shells. The size distribution of live *A. wheeleri* in the Kiamichi River is skewed to the left (Sokal and Rohlf, 1981) (Fig. 4) with more large individuals and fewer small individuals than one would expect from a statistically normal distribution. The size distribution of relict shells (Fig. 4) follows a more normal distribution, with a greater proportion of smaller individuals than in the live population. Looking at these shell length data alone, one would conclude that the size distribution of *A. wheeleri* in the Kiamichi River has changed over time and recruitment has decreased.

There may be problems with comparing the size distributions of relict shells with live shells. Relict shells from museum collections may have been collected in a size-biased manner because the rate at which dead shells are moved by currents, disintegrate through time, and are collected, could all be functions of shell size. Nevertheless, we would predict that these forces would make it more likely for collectors to find large relict shells rather than small relict shells. Because we found that our "population" of relict shells was generally smaller than our population of live mussels, such a size bias would actually make our demographic estimates conservative.

External annular rings have long been used to determine mussel age and growth rates. Recently this technique has been criticized as being replete with problems (Neves and Moyer, 1988; Downing *et al.*, 1992). Natural erosion and corrosion of shells makes it difficult to distinguish true from false annuli. For example, false annuli can be formed by the incorporation of small substrate particles into mussel shells. It is difficult to count closely deposited growth lines near the margins of old shells. This produces an underestimate of shell age that becomes more erroneous with shell age. Downing *et al.* (1992) studied populations of *Lampsilis radiata* (Gmelin, 1791) and *Anondonta grandis* in an oligotrophic lake. In these populations, many mussels showed no new external annuli at all, even several years after individual animals had been marked. They concluded that estimates of growth based on shell annuli consistently overestimated real shell growth. In addition, shell size and growth rates are linked to environmental conditions. For example, some species form narrower shells in coarser substrates (Hinch *et al.*, 1989) or grow faster in sand than in mud (Hinch *et al.*, 1986). However, taking into account the large margin of error in using this method, most *Arkansia wheeleri* encountered in the Kiamichi River were old. Using this method, the youngest live *A. wheeleri* specimen we encountered was approximately 12 years of age. No juveniles were encountered. Both types of data, shell-size distributions and ages predicted from external annuli, demonstrated that most *A. wheeleri* encountered in the Kiamichi River were old.

Because of its rarity, the reproductive biology of *Arkansia wheeleri* remains unknown. Like other anodontines, it is probably bradytictic. The closest relative of *A. wheeleri*, *Arcidens confragosus* (Say, 1829), becomes gravid in the fall and releases glochidia in the spring

(Clarke, 1981). We were unable to obtain any gravid *A. wheeleri* and thus obtained no glochidia. *A. wheeleri* glochidia are probably similar to other alasmidontine glochidia. Alasmidontine glochidia are asymmetrical and have a stylet covered with microstylets which facilitate attachment to the fish host. Glochidial releases are probably tied to natural water temperature changes in the spring and fall (Jirka and Neves, 1992).

It appears that historically, *Arkansia wheeleri* survived equally well above and below the impounded tributary to the Kiamichi River (Clarke, 1987). Historically, *A. wheeleri* occurred in at least seven sites below the tributary. However, in five years of combined sampling effort by Mehlhop and Miller (1989), 1988-1989, and ourselves, 1990-1992, only three subpopulations of *A. wheeleri* have been found below Jackfork Creek. Therefore, only three out of seven (43%) of the known subpopulations of *A. wheeleri* survive below Jackfork Creek. In contrast, three out of four (75%) of the historical locations of *A. wheeleri* above Jackfork Creek have been confirmed and five new locations have been discovered. No new locations have been discovered below Jackfork Creek despite intensive survey efforts. In addition, the relative abundance of *A. wheeleri* is slightly higher above Jackfork Creek than below, although these differences are not statistically significant. Unfortunately, we have no historical abundance data for *A. wheeleri* in the Kiamichi River.

The greatest threats to the continued existence of *Arkansia wheeleri* in the Kiamichi River are land use changes, including further impoundment of the river, water transfers, timber harvesting, and pollution from agricultural and industrial development (Neves, 1993; Mehlhop and Vaughn, 1994). This species is also threatened by the invasion of exotic bivalve species, particularly the zebra mussel, *Dreissena polymorpha* (Pallas, 1771). *D. polymorpha* is now found in the Arkansas River system in Oklahoma. The high dispersal capabilities of this species make it highly probable that it will invade the Red River system, including the Kiamichi River, in the near future (French, 1990).

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Infestations of glochidia on fishes in the Barren River, Kentucky

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Abstract. We collected fish monthly from the Barren River, Kentucky, to assess glochidial infestations. Glochidia were encysted on 4.1% of the 2,510 fish of 43 species examined. Twenty-five fish species in 11 families were infested; 14 of these species are not known to be hosts of any of the 27 mussel species (Unionidae) occurring in the Barren River. Amblemine glochidia occurred on 19 species of fish. Eight species of fish were infested with anodontine glochidia, while lampsiline glochidia occurred on only five species. Differences in the degree of host specificity were striking among the Ambleminae. Glochidia of *Amblema plicata* (Say, 1817) occurred on 12 species of fish, whereas those of *Quadrula pustulosa* (I. Lea, 1831) were found only on channel catfish [*Ictalurus punctatus* (Rafinesque, 1818)]. Overlap in host fishes occurred between the Ambleminae and the other subfamilies, but not between the Anodontinae and Lampsilinae. Potential new hosts are identified for *Lasmigona complanata* (Barnes, 1823), *Lasmigona costata* (Rafinesque, 1820), *Megalonaias nervosa* (Rafinesque, 1820), *A. plicata*, and *Pleurobema* spp.

The life cycle of most freshwater mussel species (Unionidae) includes a parasitic larval stage (glochidium). Glochidia develop in the gills of female mussels and are discharged into the water. Once free, they must attach to a suitable host or die. Glochidia of most mussel species parasitize fish. Some species are host specific, using a single host; others parasitize as many as 25 fish species (Gordon and Layzer, 1989). Glochidia that contact a suitable fish host usually attach to gills or fins and become encysted in fish tissue. Although host fish play a vital role in the life cycle of freshwater mussels, hosts of most mussel species are unknown (Fuller, 1974; Hoggarth, 1992).

Some mussel species can maximize the likelihood of glochidial attachment by attracting fish. For instance, the mantle of *Lampsilis cardium* closely resembles a small fish (Kraemer, 1970). Presumably, this "lure" attracts their host fishes which are piscivorous. Glochidia of other mussel species are released in packets (conglutinates) which can resemble aquatic insects often preyed upon by fish (Stein, 1971; Gordon and Layzer, 1989). Conglutinates can result in higher intensities of glochidial infestations (Neves and Widlak, 1988). Released anodontine glochidia are suspended in the water column by mucus strands and left to drift into contact with a host (Stein, 1971). This means of dispersal is augmented by the tremendous number of glochidia (up to 3.5 million) which can be released by a single female (Surber, 1912). Despite these adaptations, apparently few glochidia successfully attach to a host. Neves and Widlak (1988) found only 14% of 4,800 fish examined had encysted glochidia. Holland-Bartels and Kammer (1989) reported glochidial infestations on just 4% of 2,000 fish examined from June through August. Although not all species examined may have been hosts, these low rates of infestation suggest that host abundance can play an important role in determining reproductive success.

This study examines glochidial infestations by a diverse assemblage of freshwater mussels in the presence of a diverse fish fauna. Differences in host specificity within and among mussel subfamilies are examined. Potential new hosts are identified but will require confirmation by induced infestation experiments.

MATERIALS AND METHODS

The study was conducted on a 5-km reach of the Barren River immediately downstream from Lock and Dam 1, Warren County, Kentucky. Five 150-m long sites were established in riffle, run, and pool habitats. Mussel species composition was evaluated at each site in 1991 by timed diving. Two divers, either snorkeling or using SCUBA equipment, collected mussels at each site for 30 min. Mussels were identified to species and returned to the site. Except for *Pyganodon grandis*, nomenclature follows Turgeon *et al.* (1988).

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Fish were collected at each site from October 1990 to September 1991 in all months except November 1990. A variety of gear was used depending upon water levels. Experimental gill nets were 45.7 m long with six equally sized panels of mesh from 1.9-6.4 cm bar measure. Two sizes of hoop nets were used: large nets had 92-cm diameter hoops, a front mesh of 5.1 cm, and back mesh of 3.8 cm; small nets had 51-cm diameter hoops and 3.8 cm mesh throughout. Large nets were used in areas of sufficient depth to completely submerge the hoops. In shallower sites, the small nets were used. Both baited and unbaited sets were made and the time of each recorded. A 30.5-m long seine with 6.4 mm mesh was used on the four shallowest sites when water levels allowed. The number of seining locations established within a station was determined by the habitat present. A 6.1-m long seine with 6.4 mm mesh was used on several dates when water levels prevented use of the large seine. Electrofishing was conducted with a boat-mounted direct-current unit. Each site was sampled by making three passes upstream. One pass was made along each bank and one in the center of each site. All fish collected were retained. Small individuals were fixed in 10% buffered formalin in the field and transferred to 70% ethanol in the laboratory. Large individuals were placed on ice and then frozen within 48 hr. Common and scientific names of fishes follow Robins *et al.* (1991).

The maximum number of fish examined for glochidial infestations was restricted to 20 individuals per species for each gear type used at a station on each sampling date. Fish were examined under a dissecting microscope at 10-70X magnification. All gill arches and fins were removed from fish greater than approximately 100 mm in length and examined individually. Smaller fish were examined whole. Glochidia were removed with a probe and preserved in 70% ethanol. The locations of glochidia on each infested fish were recorded. Length, height, and hinge length of each glochidium were measured to the nearest 5 µm with an ocular micrometer in a compound microscope (100 X). Length was the maximum distance between the anterior and posterior shell margins. Height was measured from the hinge to the ventral margin. Hinge length was defined as the distance between the points where the hinge intersected with the anterior and posterior shell margins. Shape was used to identify glochidium to subfamily; misidentification of subfamily was unlikely because differences in shape were usually distinct. Dimensions of glochidium were compared to those of glochidia obtained from gravid mussels and to measurements reported in the literature for identification of species. This method did not account for potential differences in glochidia sizes among populations; however, when species dimensions were not different, identification was restricted to subfamily.

RESULTS

Twenty-seven species of mussels including the federally endangered *Pleurobema plenum* were collected from the study area (Table 1). Thirteen species of Ambleminae were collected; *Amblema plicata* comprised 40% of the total number of mussels collected and *Megalonaias nervosa* comprised 11%. *Actinonaias ligamentina* (8%) and *Ptychobranchus fasciolaris* (7%) were the most common of the 10 species of Lampsilinae collected. Of the four species of Anodontinae present, *Lasmigona costata* and *L. complanata* were most abundant; together they comprised 5% of the mussels collected.

We collected and examined only 281 fish from December through May because the high discharge from the Barren River Lake, located 40 km upstream, affected our sampling efficiency. During the summer and fall, we examined 164-748 fish per month. Overall, 6,736 fish of 43 species were collected and 2,510 of these were examined for glochidial infestations. Twenty-five species of fish in 11 families were infested (Table 2). Fourteen of these species have not been identified as hosts for any mussel species occurring in the Barren River. Glochidia were not found on seven fish species that are known hosts for one or more mussel species present; however, six of these fish species were rarely collected.

Although hooks on glochidial valves are characteristic of Anodontinae, they were not easily observable on closed glochidia. Nonetheless, anodontine glochidia were distinctive because of their triangular shape. Moreover, anodontine glochidia were nearly always larger in all dimensions than amblemine and lampsiline glochidia (Table 3). Glochidia of Lampsilinae and Ambleminae overlapped considerably in size of each dimension measured; however, individual species in these subfamilies did not overlap in all three dimensions. For instance, valve lengths and heights of *Megalonaias nervosa* and *Ellipsaria lineolata* were similar, but hinge lengths differed considerably. In general, glochidia of Ambleminae tended to be rounder in shape than glochidia of Lampsilinae.

Amblemine glochidia occurred on 19 species of fish in 10 families (Table 2). Anodontine glochidia occurred on eight species of fish with those of the Lampsilinae infesting just five species. Four fish species, longnose gar *(Lepisosteus osseus)*, gizzard shad *(Dorosoma cepedianum)*, golden redhorse *(Moxostoma erythrurum)*, and flathead catfish *(Pylodictis olivaris)* were used by anodontine and amblemine species. Infestations of lampsiline and amblemine species occurred on channel catfish *(Ictalurus punctatus)* and spotted bass *(Micropterus punctatus)*; however, infestations by anodontine and lampsiline species did not occur on the same fish species. In three instances, anodontine glochidia occurred along with glochidia of *Megalonaias*

Table 1. Mussel species (Unionidae) collected from the Barren River during 1991.

Subfamily	Species	N	Relative Abundance (%)
Anodontinae	*Arcidens confragosus* (Say, 1829)	3	0.6
	Pyganodon grandis (Say, 1829)	1	0.2
	Lasmigona complanata (Barnes, 1823)	11	2.2
	L. costata (Rafinesque, 1820)	13	2.6
	Subfamily Total	28	5.5
Ambleminae	*Amblema plicata* (Say, 1817)	201	39.6
	Cyclonaias tuberculata (Rafinesque, 1820)	1	0.2
	Elliptio crassidens (Lamarck, 1819)	12	2.4
	Fusconaia flava (Rafinesque, 1820)	2	0.4
	F. subrotunda (I. Lea, 1831)	4	0.8
	Megalonaias nervosa (Rafinesque, 1820)	56	11.0
	Pleurobema cordatum (Rafinesque, 1820)	17	3.4
	P. plenum (I. Lea, 1840)	8	1.6
	P. pyramidatum (I. Lea, 1840)	2	0.4
	P. coccineum (Conrad, 1834)	2	0.4
	Quadrula pustulosa (I. Lea, 1831)	13	2.6
	Q. quadrula (Rafinesque, 1820)	14	2.8
	Tritogonia verrucosa (Rafinesque, 1820)	12	2.4
	Subfamily Total	344	67.7
Lampsilinae	*Actinonaias ligamentina* (Lamarck, 1819)	38	7.5
	Ellipsaria lineolata (Rafinesque, 1820)	18	3.5
	Lampsilis cardium (Rafinesque, 1820)	4	0.8
	L. ovata (Say, 1817)	5	1.0
	Leptodea fragilis (Rafinesque, 1820)	3	0.6
	Ligumia recta (Lamarck, 1819)	1	0.2
	Obliquaria reflexa (Rafinesque, 1820)	2	0.4
	Potamilus alatus (Say, 1819)	24	4.7
	Ptychobranchus fasciolaris (Rafinesque, 1820)	37	7.3
	Truncilla truncata (Rafinesque, 1820)	2	0.4
	Subfamily Total	136	26.8
	Overall Total	506	

nervosa on the same individual (longnose gar, gizzard shad, and flathead catfish). An individual golden redhorse and a sauger *(Stizostedion canadense)* were infested with glochidia of Anodontinae and those of *Amblema plicata.* Glochidia of *A. plicata* and another amblemine species occurred on one mooneye *(Hiodon tergisus).*

Ambleminae displayed varying levels of host specificity (Table 4). Glochidia of *Amblema plicata* were found on 12 fish species and *Megalonaias nervosa* on eight fish species. In contrast, glochidia of *Quadrula pustulosa* occurred only on channel catfish and glochidia of *Pleurobema* spp. only on mooneye and steelcolor shiner *(Cyprinella whipplei).* Seven known amblemine hosts were infested while 12 fish species previously not identified as hosts of the Ambleminae occurring in the Barren River, also were infested (Table 4).

Glochidia of both *Lasmigona complanata* and *L. costata* occurred on gizzard shad and river redhorse *(Moxostoma carinatum)* while glochidia of either *Pyganodon grandis* or *Arcidens confragosus* occurred on four fish species. None of the fishes infested with anodontine glochidia were known hosts of an anodontine species occurring in the Barren River.

Lampsiline glochidia were rarely found on the fish examined. Glochidia of *Potamilus alatus* infested freshwater drum *(Aplodinotus grunniens)*, a known host. Glochidia of other Lampsilinae occurred on four fish species, none of which are known hosts of any lampsiline species collected.

Most infested fish carried few encysted glochidia (generally 1-5); however, one freshwater drum, captured in April, was infested with 232 *Potamilus alatus* glochidia. This was the only instance of such a high intensity of infestation.

Glochidia of *Megalonaias nervosa* occurred as frequently on fins as on gills of fish, particularly longnose gar and gizzard shad. Anodontine glochidia occurred more frequently on gills (92%) than on fins while lampsiline glochidia occurred only on gills.

Table 2. Prevalence of glochidial infestations on fishes collected from the Barren River from October 1990 to September 1991. Asterisks indicate fish species which are known hosts of one or more mussel species in the Barren River.

Family Species	N	Percent Infested (by Subfamily)		
		Ambleminae	Anodontinae	Lampsilinae
Lepisosteidae				
*_Lepisosteus osseus_ (Linné, 1758)	29	24	3	–
L. oculatus (Winchell, 1864)	2	–	–	–
Hiodontidae				
Hiodon tergisus (Lesueur, 1818)	11	45	–	–
Clupeidae				
*_Dorosoma cepedianum_ (Lesueur, 1818)	234	9	2	–
Cyprinidae				
*_Pimephales notatus_ (Rafinesque, 1820)	133	–	–	–
*_Cyprinus carpio_ Linné, 1758	3	–	–	–
Notropis atherinoides Rafinesque, 1818	307	< 1	–	–
N. rubellus (Agassiz, 1850)	3	–	–	–
Cyprinella spilopterus (Cope, 1868)	357	< 1	–	–
C. whipplei Girard, 1856	453	1	–	–
Erimystax dissimilis (Kirtland, 1840)	46	2	–	–
Catostomidae				
Moxostoma duquesnei (Lesueur, 1817)	22	5	–	–
M. erythrurum (Rafinesque, 1818)	55	5	2	–
M. carinatum (Cope, 1870)	17	–	24	–
M. macrolepidotum (Lesueur, 1817)	46	–	2	–
M. anisurum (Rafinesque, 1820)	17	–	–	–
Hypentelium nigricans (Lesueur, 1817)	16	6	–	–
Minytrema melanops (Rafinesque, 1820)	12	–	–	–
Ictiobus bubalus (Rafinesque, 1818)	4	–	–	–
Carpiodes carpio (Rafinesque, 1820)	4	–	25	–
C. cyprinus (Lesueur, 1817)	3	–	–	–
*_C. velifer_ (Rafinesque, 1820)	2	–	–	–
Esocidae				
Esox masquinongy Mitchell, 1824	1	–	–	–
Ictaluridae				
*_Ictalurus punctatus_ (Rafinesque, 1818)	25	12	–	16
*_Pylodictis olivaris_ (Rafinesque, 1818)	3	67	33	–
Cyprinodontidae				
Fundulus notatus (Rafinesque, 1820)	1	–	–	–
Poeciliidae				
Gambusia affinis (Baird and Girard, 1853)	19	–	–	–
Atherinidae				
*_Labidesthes sicculus_ (Cope, 1865)	181	–	–	< 1
Cottidae				
*_Cottus carolinae_ (Gill, 1861)	4	–	–	–
Percichthyidae				
*_Morone chrysops_ (Rafinesque, 1820)	1	100	–	–
Centrarchidae				
*_Lepomis gulosus_ (Cuvier, 1829)	3	67	–	–
*_L. macrochirus_ Rafinesque, 1819	148	< 1	–	–
L. megalotis (Rafinesque, 1820)	67	–	–	2
*_Ambloplites rupestris_ (Rafinesque, 1817)	1	–	–	–
*_Poxomis annularis_ Rafinesque, 1818	4	75	–	–
*_P. nigromaculatus_ (Lesueur, 1829)	2	–	–	–
Micropterus punctatus (Rafinesque, 1819)	66	2	–	5
*_M. salmoides_ (Lacepede, 1802)	1	–	–	–
Percidae				
Etheostoma blennioides Rafinesque, 1819	1	–	–	–
Percina caprodes (Rafinesque, 1818)	24	4	–	–
P. phoxocephala (Nelson, 1876)	1	–	–	–
*_Stizostedion canadense_ (Smith, 1834)	5	–	20	–
Sciaenidae				
*_Aplodinotus grunniens_ Rafinesque, 1819	73	12	–	–

Table 3. Dimensions of glochidia measured in this and other studies as cited (ranges are mean ± 1 SD).

	Dimensions (µm)			
Family Subfamily	Length	Height	Hinge Length	Citation
Anodontinae				
Pyganodon grandis	350-362	352-358	250-258	Hoggarth (1988)
	366-380	371-396	272-281	Current Study
Arcidens confragosus	354-364	353-355	239-253	Hoggarth (1988)
Lasmigona complanata	290-296	295-309	195-208	Hoggarth (1988)
L. costata	341-347	363-375	239-243	Hoggarth (1988)
	353-377	380-414	249-271	Current Study
Ambleminae				
Amblema plicata	200	200	–	Surber (1912)
	185-200	195-215	–	Howard (1914)
Cyclonaias tuberculata	348-362	288-300	127-139	Jirka and Neves (1992)
Elliptio crassidens	130	150	–	Ortmann (1912)
	150	160	–	Surber (1915)
Fusconaia flava	150	150	–	Ortmann (1912)
F. subrotunda	130	150	–	Ortmann (1912)
Megalonaias nervosa	254-268	341-351	147-153	Hoggarth (1988)
Pleurobema cordatum	140	150	–	Yokley (1972)
	160	175	–	Surber (1915)
P. coccineum	160	160	–	Surber (1915)
Quadrula pustulosa	233-245	292-303	98-106	Current Study
	230	300	–	Lefevre and Curtis (1912)
Q. quadrula	85	90	–	Surber (1915)
Tritogonia verrucosa	87-93	98-102	43-45	Hoggarth (1988)
	119-125	106-112	46-52	Jirka and Neves (1992)
Lampsilinae				
Actinonaias ligamentina	245-263	221-235	123-135	Jirka and Neves (1992)
	220	243	125	Hoggarth (1988)
Ellipsaria lineolata	248-258	316-354	87-109	Curent Study
	232-242	316-326	87-94	Hoggarth (1988)
Lampsilis cardium	244-254	277-289	107-115	Hoggarth (1988)
L. ovata	232	270-278	113-119	Hoggarth (1988)
	303-315	257-271	117-125	Jirka and Neves (1992)
Leptodae fragilis	71-73	80-82	30-36	Hoggarth (1988)
Ligumia recta	205-217	257-263	106-112	Hoggarth (1988)
Obliquaria reflexa	214-220	213-223	118-126	Hoggarth (1988)
Potamilus alatus	213-225	370-386	96-108	Hoggarth (1988)
Ptychobranchus fasciolaris	170-176	180-194	78-88	Hoggarth (1988)
Truncilla truncata	60	70	–	Surber (1912)

DISCUSSION

Most glochidia encysted on fish were those of the most abundant mussel species in the Barren River. Glochidia of *Amblema plicata*, the most frequently collected mussel, occurred on 12 species of fish in 7 families. Only two of these species have been reported as hosts (see Gordon and Layzer, 1989; Watters, 1994). Although laboratory trials of induced infestations are needed to confirm host suitability, the diversity of known hosts for *A. plicata* suggests that many additional fish species could be suitable hosts. In contrast, we did not find glochidia of *Potamilus alatus* encysted on any species other than freshwater drum, its only known host (Howard, 1913).

The small number of fish collected in the winter and spring most likely resulted in the low prevalence of lampsiline infestations on fish we examined. The relatively high frequency of fish infested with glochidia of *Megalonaias nervosa* during the winter probably resulted from the long encystment period (2-6 months) typical of this species (Howard, 1914).

The low prevalence of infestations on fins by anodontine glochidia was unexpected. The hooks of anodontine glochidia are thought to be an adaptation for

Table 4. Fish species examined and percent infested by mussel species in the Barren River from October 1990 to September 1991. Asterisks indicate known hosts.

Mussel species	Fish Species	N	% Infested
Anodontinae			
Lasmigona complanata	_Lepisosteus osseus_	29	3
	Dorosoma cepedianum	234	< 1
	Moxostoma carinatum	17	18
	Stizostedion canadense	5	20
L. costata	_Dorosoma cepedianum_	234	< 1
	Moxostoma carinatum	17	6
Anodontinae spp.	_M. erythrurum_	55	2
	M. macrolepidotum	46	2
	Carpiodes carpio	4	25
	Pylodictis olivaris	3	33
Ambleminae			
Megalonaias nervosa	_Lepisosteus osseus_	29	24
	*_Dorosoma cepedianum_	234	6
	*_Pylodictis olivaris_	3	67
	*_Morone chrysops_	1	100
	Lepomis gulosus	3	67
	*_Pomoxis annularis_	4	75
	Micropterus punctulatus	66	2
	*_Aplodinotus grunniens_	73	1
Amblema plicata	_Hiodon tergisus_	11	36
	Notropis atherinoides	307	< 1
	Cyprinella splioptera	357	< 1
	C. whipplei	453	< 1
	Erimystax dissimilis	46	2
	Moxostoma duquesnei	22	5
	M. erythrurum	55	5
	Hypentelium nigricans	16	6
	*_Ictalurus punctatus_	25	4
	*_Lepomis macrochirus_	148	< 1
	Percina caprodes	24	4
	Aplodinotus grunniens	73	10
Quadrula pustulosa	*_Ictalurus punctatus_	25	8
Pleurobema spp.	_Hiodon tergisus_	11	9
	Cyprinella whipplei	453	< 1
Ambleminae spp.	_Aplodinotus grunniens_	73	1
Lampsilinae			
Potamilus alatus	*_Aplodinotus grunniens_	73	3
Lampsilinae spp.	_Ictalurus punctatus_	25	16
	Labidesthes sicculus	181	< 1
	Lepomis megalotis	67	2
	Micropterus punctulatus	66	5

attachment to fins (Lefevre and Curtis, 1912). However, the higher prevalence of infestations on gills observed in this study and by Wiles (1975) suggests that the hooks are simply an adaptation for attachment, regardless of the location on the fish.

Catostomids have been infrequently identified as glochidial hosts; however, we found glochidia of _Amblema plicata, Lasmigona complanata, L. costata_, and Anodontinae spp. encysted on several species of Catostomidae. Because steelcolor shiners and mooneyes were infested with glochidia of _Pleurobema_ spp., they should be tested as potential hosts for the federally endangered _Pleurobema plenum._

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Ecology of infaunal Mollusca in south Texas estuaries

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Abstract. The ecology of Texas estuaries is strongly influenced by latitudinal ecotones that exist along the northwestern Gulf of Mexico coastline. Long-term studies were conducted in four of the seven major estuarine ecosystems in Texas. The objective was to determine the role of climatic variability and concordant differences in freshwater inflow among the ecosystems in structuring benthic infaunal communities and maintaining secondary production. Mollusks are prominent members of the infauna in all benthic habitats of Texas estuaries. The abundance, biomass, and community structure of mollusks was measured along salinity gradients within the four south Texas estuaries. Infaunal samples were collected by divers using small (6.7 cm diameter) cores (so larger epibenthic mollusks were not collected). Overall, these Texas estuaries had a mean of 14 species of infaunal mollusks, with mean abundance of 7,500 individuals/m^2, and mean biomass of 2.4 g/m^2. Freshwater inflow is the dominant factor regulating variability of molluscan communities. Salinity is a surrogate for inflow, therefore, there are zoogeographic patterns within and among estuaries related to salinity patterns. There are seasonal, interannual, and latitudinal patterns of inflow, and these patterns are apparently regulating community structure, population dynamics, and secondary production in Texas estuaries. Recent water projects to enhance the amount of freshwater flowing into estuaries appear to have had an effect and have increased the number of mollusks in those areas. However the projects occurred during a naturally wet period, so it is difficult to differentiate natural versus anthropogenic changes. The response of mollusks to natural gradients and man-induced changes of freshwater inflow demonstrate the importance of this factor in regulating benthic communities.

A major component of benthic ecosystems in Texas estuaries, as is true elsewhere, is the Mollusca. Molluscan biomass dominates the macroinfauna in Lavaca, San Antonio, Corpus Christi, and Nueces Bays (Kalke and Montagna, 1991; Montagna and Kalke, 1992). During peak recruitment events, Mollusca can also dominate population abundance. However, differences in population size and community structure exist within and among Texas Bays.

There are seven major estuarine systems along 600 linear kilometers of coastline. The estuaries of Texas are remarkably diverse in spite of similar physiography (Fig. 1). This is due to a climatic gradient, which influences freshwater inflow. The gradient of decreasing rainfall, with concomitant freshwater inflow from north to south, is the most distinctive feature of the coastline (Table 1). Along this gradient, rainfall decreases by a factor of two, but inflow balance decreases by almost two orders of magnitude. The inflow patterns appear to group into four distinct types of estuaries that vary by about an order of magnitude each (Table 1). Each estuary-type also has distinctly different timing of peak inflow events. The northern estuaries receive peak inflow during the spring, the central estuaries are bimodal receiving peak inflows during the spring and fall, and the southernmost estuaries receive peak inflows during the fall (Texas Department of Water Resources, 1982). These distinct patterns are very important, because growth, reproduction, and migration of many species are keyed to seasonal events. The timing and magnitude of inundation is believed to regulate finfish and shellfish production (Texas Department of Water Resources, 1982).

We have been conducting long-term studies in four of the seven estuaries to determine the role of freshwater inflow in maintaining benthic productivity. The primary purpose of the current study was to determine the degree of influence of freshwater inflow in regulating zoogeographic differences of molluscan population size and community structure within and among Texas estuaries. The secondary purpose of this study was to assess the effects of two major water projects designed to increase freshwater inflows to estuaries to maintain or enhance productivity. One project was a mandated freshwater release schedule from a dam and the other was a diversion of river water to an estuary. The focus in this manuscript is on the infaunal mollusks.

METHODS

All seven Texas estuaries have similarities in their structure and physiography (Fig. 1). Barrier islands are parallel to the mainland along most of the coast. Between the islands and the mainland there are lagoons. The

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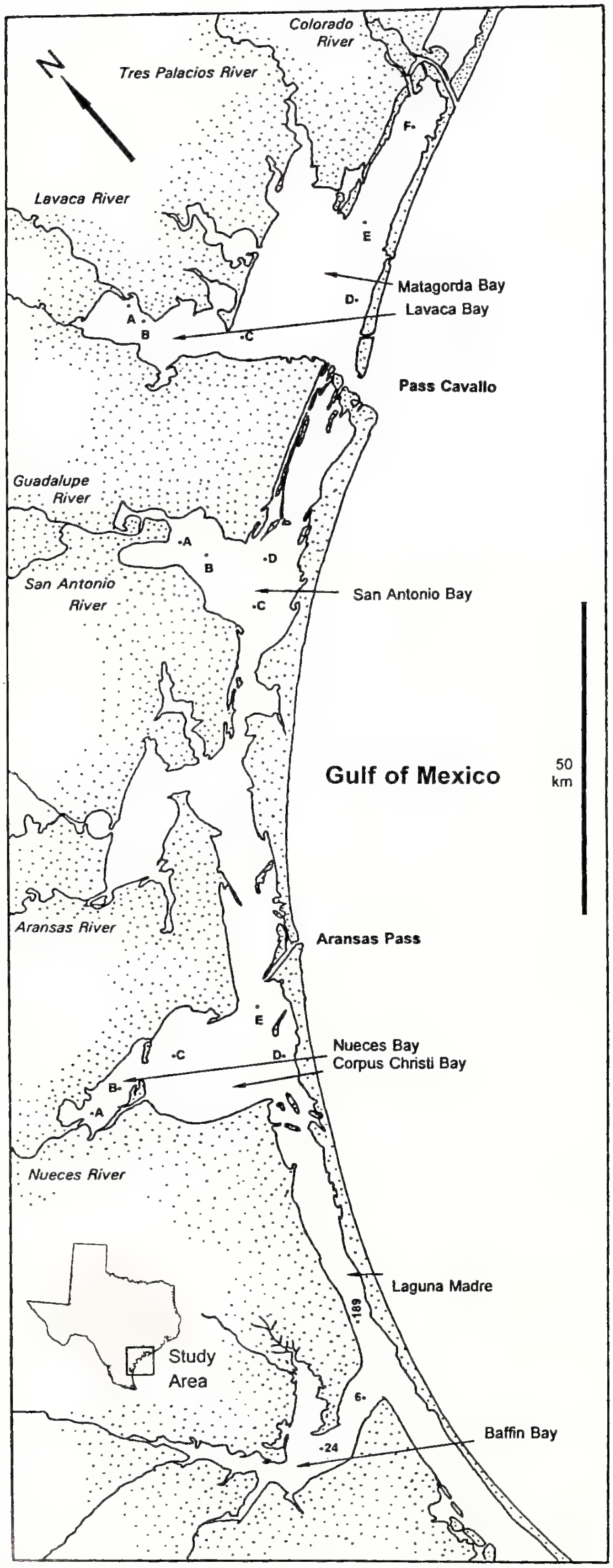

Fig. 1. Location of south Texas estuaries and sampling stations.

Table 1. Gradients in Texas estuaries. Listed from north to south: area at mean low tide (Diener, 1975), mean annual rainfall (1951-1980; Larkin and Bomar, 1983), mean annual freshwater inflow balance (1941-1976; Texas Department of Water Resources, 1982), and mean annual commercial harvest (1962-1987; Texas Parks and Wildlife Department, 1988).

				Commercial Harvest	
Estuary	Area (km^2)	Rainfall (cm/yr)	Inflow (10^6 m^3/yr)	Finfish (10^3 kg/yr)	Shellfish (10^3 kg/yr)
Sabine-Neches	183	142	16,107	5	332
Trinity-San Jacinto	1,416	112	12,284	190	4,060
Lavaca-Colorado	1,158	102	3,242	100	2,076
Guadalupe	551	91	2,545	80	1,545
Mission-Aransas	453	81	190	207	1,453
Nueces	433	76	509	151	544
Laguna Madre	1,139	69	-947	834	147

lagoons are interrupted by drowned river valleys that form the bay and estuarine systems. There are Gulf inlets through the barrier islands, which connect the sea with the lagoon behind the island. The lagoon opens to a large primary bay. There is a constriction between the primary bay and the smaller secondary bay. The river flows into the secondary bay. Primary bays have greater marine influence and secondary bays have greater freshwater influence. So, as well as a latitudinal climatic gradient, there is a longitudinal salinity gradient within each estuary.

The similarity of the Texas estuaries allowed us to design a sampling program where we could use statistical control on confounding factors, *e.g.* Gulf exchange, circulation patterns, and alterations by humans. Four to six stations were chosen in each estuary (Table 2, Fig. 1) employing the same spatial sampling design that has been employed in previous studies of Texas estuaries (Montagna and Kalke, 1992). Two replicate stations (A and B) were in the secondary bay where freshwater influences are greatest. Two other replicate stations (C and D) were in the primary bay where marine influences are greatest. By using two stations in the freshwater-influenced zone and two stations in the marine-influenced zone, we were replicating effects at the treatment level and avoiding pseudoreplication (Hurlbert, 1984). There has been a diversion of the Colorado River into the east arm of Matagorda Bay, so we located two additional stations (E and F) there. The stations in Laguna Madre are located using a similar strategy. Two stations were located in Baffin Bay (6 and 24), and two stations were located in Laguna Madre in a seagrass bed (189G) and an unvegetated sand patch (189S) (Fig. 1).

Two major water projects were initiated during the course of this study. The purpose of both projects was to increase freshwater inflows to bays to enhance secondary productivity. In 1990, the Texas Water Commission

Table 2. Location of sampling stations and sampling periods.

Estuary	Bay	Name	Stations	Period
Lavaca-Colorado	Secondary	Lavaca Bay	A	1984-1994
	Secondary	Lavaca Bay	B	1988-1994
	Primary	Matagorda Bay	C, D	1988-1994
	Diversion	East Matagorda Bay	E, F	1993-1994
Guadalupe	Secondary	Upper San Antonio Bay	A, B	1987-1994
	Primary	Lower San Antonio Bay	C, D	1987-1994
Nueces	Secondary	Nueces Bay	A, B	1988-1994
	Primary	Corpus Christi Bay	C, D	1988-1994
	Primary	Corpus Christi Bay	E	1990-1994
Laguna Madre	Secondary	Baffin Bay	6, 24	1989-1993
	Primary	Laguna Madre	189G, 189S	1989-1993

ordered the City of Corpus Christi to release 151,000 ac-ft/yr (1.86×10^8 m^3/yr) to the Nueces Estuary from the Choke Canyon/Lake Corpus Christi reservoir system. The releases were mandated, because the City had not been releasing water. Stations A and B in Nueces Bay were used to assess the effects of this project (Fig. 1). The Colorado River was diverted into the eastern arm of Matagorda Bay by the creation of a flood diversion channel in 1991 and a dam in the river channel below the point of diversion in 1992. This project has diverted Colorado River water from the Gulf of Mexico into the eastern arm of Matagorda Bay. Stations E and F were sampled to assess the effect of this diversion into Matagorda Bay (Fig. 1). The current study is not a complete assessment of the efficacy of these two projects.

Replicate sediment samples (3) were taken within a 2 m radius at each of the stations in each estuary four times per year. Abundance and community structure were measured using the standard techniques that we (Montagna and Kalke, 1992) have been using since 1984. This includes sectioning 6.7 cm diameter cores (at 0-3 cm, and 3-10 cm) to examine the vertical distribution of infauna. Animals were then extracted using a 0.5 mm sieve, enumerated, and identified. Taxonomic authorities used were Abbott (1974), Turgeon *et al.* (1988), and Andrews (1992). Principal components analysis (PCA) was performed on all data sets to determine the relationship among stations in terms of species composition. Species composition was then pooled by bay within each estuary, and PCA was performed on these data to determine relationships among bays. Hydrographic data were recorded at each station using a Hydrolab Surveyor II (Hydrolab, Inc.). These measurements included: salinity, conductivity, temperature, dissolved oxygen, oxidation-reduction potential, pH, and depth. Salinity is reported as practical salinity units (psu).

RESULTS

SALINITY REGIMES

There were large differences in salinity from year to year in all estuaries (Fig. 2). The years 1985-1986 and 1992-1993 were wet periods with concordant low salinities. These wet periods occur during periods when an El Niño event is occurring in the western Pacific Ocean. The intervening time between El Niño events is dry. Texas suffers through a series of flood and drought periods regulated by global climatic events. There are generally lower salinities in the spring and higher salinities in the summer, because of seasonal inflow and evaporation patterns.

Salinity in the Lavaca-Colorado Estuary ranged from 0-36 psu (Fig. 2). The lowest salinities always occurred in the secondary bay at stations A and B. After the diversion of the Colorado River, Stations E and F exhibited low salinities that are more typical of the secondary bay.

Salinity in the Guadalupe Estuary ranged from 0-32 psu (Fig. 2). During flood periods, this estuary is uniformly low (0-10 psu) in salinity. This is unusual compared to other Texas estuaries. It is caused by the high rate of inflow into a relatively small estuary (Table 1). The high turnover rate and low rate of exchange of marine water with the Gulf of Mexico exacerbate this trend. During extreme flooding the entire estuary can be at or near 0 psu. During drought periods, there can be a gradient of salinity.

Salinity in the Nueces Estuary ranged from 2-45 psu

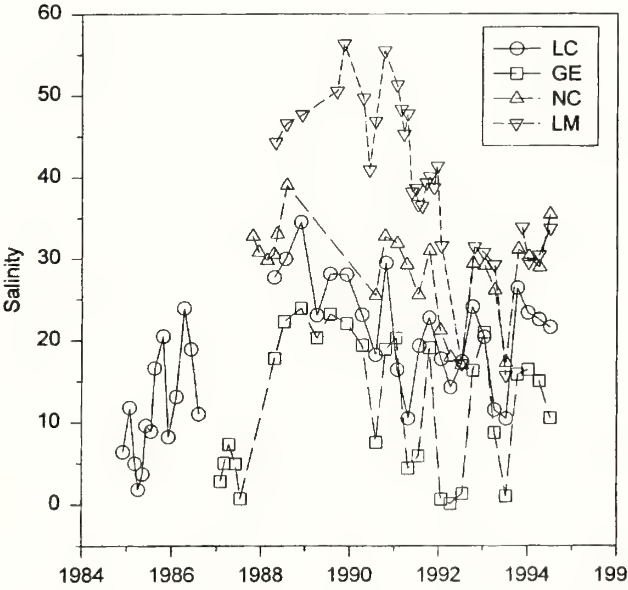

Fig. 2. Mean bottom salinity (psu) at all stations during each sampling period. (GE = Guadalupe Estuary; LC = Lavaca-Colorado Estuary; LM = Laguna Madre-Baffin Estuary; NC = Nueces Estuary).

(Fig. 2). Prior to 1991, salinities in the estuary were uniform and high. In 1991, after a series of mandated freshwater releases, salinities declined in the secondary bay. Salinities in the secondary bay were much lower than in the primary bay, where they had been similar in 1987-1988. Heavy rain in 1992-1993 reduced salinity further.

Salinity in the Laguna-Baffin Estuary ranged from 10-60 psu (Fig. 2). Seasonal fluctuations are less evident in this system. Changes occur system-wide when there are large climatic events, *e.g.* the 1992-1993 El Niño event. There is little salinity gradient in this ecosystem, because freshwater inflow and exchange with the Gulf of Mexico is restricted.

COMMUNITY STRUCTURE

In the Lavaca-Colorado Estuary, stations A and B were almost identical (Fig. 3A). Station F, at the mouth of the river diversion was also similar to A and B. Stations C and E were similar, and both these stations are nearly equidistant from freshwater input and Gulf exchange. Station D, near the pass, was the most different station of all. The pattern elucidated in the PCA was driven by the greater number of species that were found in station D, near the Gulf pass (Table 3). Also, species dominance patterns were different. The dominant bivalves were from the genus *Periploma* at stations C and D, whereas *Mulinia lateralis* (Say, 1822) was dominant at stations A, B, E, and F where there is freshwater influence. Gastropod species were more uniformly distributed throughout the estuary. The dominant gastropods were *Nassarius acutus* (Say, 1822) and *Acteocina canaliculata* (Say, 1826). Bivalves were always dominant over gastropods. Gastropods were most common in Lavaca Bay where they constituted 32% of the population at station A and 49% at B. In contrast, gastropods represented only 24% in C, 14% in D, 16% in E, and 20% in F.

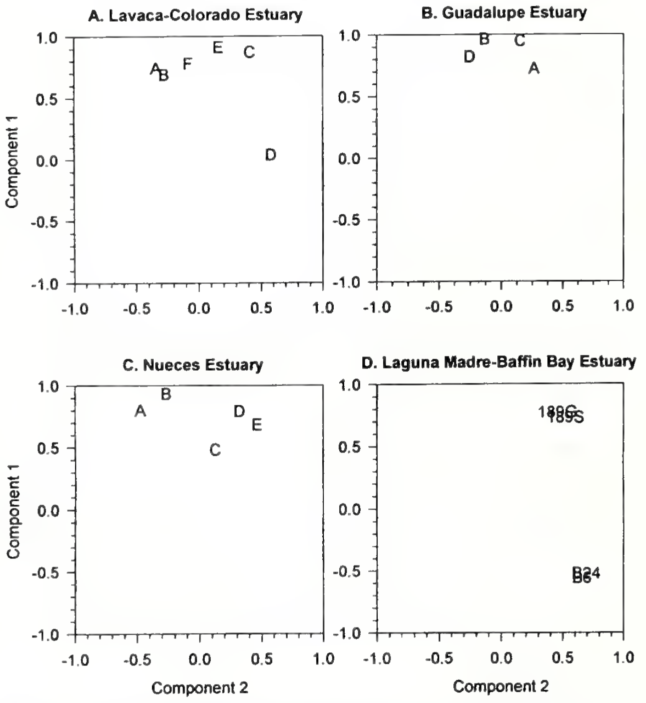

Fig 3. Principal components analysis of molluscan communities at each station over the entire study period within estuaries.

In the Guadalupe Estuary, all of the stations were somewhat alike in terms of community structure (Fig. 3B). There was more of a gradient from stations A to B to C to D in terms of abundance of individual species (Table 3). This was true for the dominant species, *e.g. Texadina sphinctostoma* (Abbott and Ladd, 1953), *Acteocina canaliculata*, and *Mulinia lateralis*. The brackish water species, *Rangia cuneata* (Sowerby, 1831) only occurred in stations A and B. In general, there were more species in the marine end of the estuary where stations C and D are located. However, there were much higher abundances of species in the freshwater end of the estuary where stations A and B are located (Table 3). In spite of these trends, the PCA indicated that there may be more affinity between stations A and C, and stations B and D may be more alike (Fig. 3B). This trend may be explained by the unusual circulation pattern in San Antonio Bay. Freshwater enters the estuary near station A, and travels southwest along the shoreline toward station C. Marine water enters the bay near station D and travels north toward station B. The species community pattern in the PCA is driven by the number of gastropods versus the number of bivalves. Gastropods were most common at station A (80% of the population) and station C (58%). In contrast, gastropods represented only 41% in B and 30% in D.

In the Nueces Estuary, stations A and B in Nueces Bay were almost identical (Fig. 3C). Stations D and E were very similar, and station C was somewhat different from all other stations. Stations D and E are nearest the Aransas Pass in Corpus Christi Bay. Station C is in the upper part of Corpus Christi Bay. The pattern elucidated in the PCA was driven by the greater number of species that were found in stations D and E, near the Gulf pass (Table 3), and some species unique to station C. In stations A and B, the dominant species were the bivalves, *Mulinia lateralis* and *Macoma mitchelli* Dall, 1895. In contrast, at stations D and E, gastropods were always dominant, where they constituted 46% of the population at station D and 33% at E. Gastropods represented only 7% in A and B, and 16% in C. Station C was different from the rest in that the dominant bivalves were from the family Nuculanidae (Table 3).

The Laguna Madre-Baffin Bay system exhibited the most varied molluscan communities within an ecosystem (Fig. 3D). This trend was due to the difference caused by

Table 3. Infaunal molluscan distribution in Texas estuaries. Mean number/m^2 for entire study period (see Table 1) at each station.

	Lavaca-Colorado Estuary						Guadalupe Estuary				Nueces Estuary					Laguna Madre-Baffin Bay			
Class/Order/Family/Species	A	B	C	D	E	F	A	B	C	D	A	B	C	D	E	189G	189S	6	24
Gastropoda																			
Gastropoda (unidentified)	95	95	95	0	0	0	12478	0	0	284	0	0	0	189	95	221	95	0	95
Mesogastropoda																			
Hydrobiidae																			
Texadina spinctostoma (Abbott & Ladd, 1953)	189	189	0	0	0	0	14683	5138	4781	934	0	0	0	0	0	0	0	0	0
Littorinidae																			
Littorina ziczac (Gmelin, 1791)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	95	0	0
Vitrinellidae																			
Vitrinella floridana Pilsbry & McGinty, 1946	0	0	0	0	0	0	0	0	0	0	0	0	0	0	95	0	0	0	0
Vitrinellidae (unidentified)	0	0	0	0	0	0	0	0	0	142	0	0	0	662	0	0	0	0	0
Caecidae																			
Caecum johnsoni Winkley, 1908	0	0	165	95	95	0	0	0	95	95	0	0	236	425	95	0	0	0	0
Caecum pulchellum Stimpson, 1851	0	0	0	0	0	95	0	95	0	95	0	0	0	0	0	2518	1395	0	0
Cerithiidae																			
Diastoma varium (Pfeiffer, 1840)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	359	95	0	0
Cerithium lutosum Menke, 1828	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	303	221	0	0
Epitoniidae																			
Epitonium sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	95	0	0	0	0	0
Calyptraeidae																			
Crepidula fornicata (Linné, 1758)	0	0	0	284	0	0	0	0	95	95	0	0	95	95	0	265	142	95	0
Neogastropoda																			
Columbellidae																			
Anachis ostreiocola Sowerby, 1882	0	0	0	0	0	0	0	0	0	0	0	0	95	0	0	95	0	0	0
Anachis semiplicata Stearns, 1873	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	158	0	0	0
Mitrella lunata (Say, 1826)	0	0	95	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Nassariidae																			
Nassarius acutus (Say, 1822)	189	158	113	189	189	95	0	0	95	0	0	0	189	95	95	95	0	0	0
Nassarius vibex (Say, 1822)	0	0	0	189	0	0	0	0	0	0	0	0	0	0	0	95	0	0	0
Pyramidelloida																			
Pyramidellidae																			
Boonea impressa (Say, 1822)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	95	0	0
Eulimastoma teres (Bush, 1885)	142	307	189	0	284	95	95	95	95	142	0	95	0	0	0	0	0	0	0
Eulimastoma sp.	0	0	0	0	189	0	567	95	0	126	95	0	0	236	0	0	0	0	0
Odostomia gibbosa (Bush, 1909)	155	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Odostomia sp.	284	189	0	0	0	0	0	0	95	0	0	0	0	0	0	0	0	0	0
Pyramidella crenulata (Holmes, 1859)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	189	95	0	0
Pyrgiscus sp.	0	142	138	95	0	0	0	0	189	165	0	0	189	284	378	340	425	0	0
Sayella crosseana (Dall, 1885)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	189	118	0	0
Cephalaspidea																			
Acteonidae																			
Rictaxis punctostriatus (C. B. Adams, 1840)	0	0	0	0	0	0	0	0	0	0	0	0	0	1135	473	0	0	529	511
Scaphandridae																			
Acteocina canaliculata (Say, 1826)	321	662	95	189	591	284	95	189	189	216	95	236	0	113	0	0	0	95	95

(continued)

Table 3. Continued.

	Lavaca-Colorado Estuary						Guadalupe Estuary				Nueces Estuary					Laguna Madre-Baffin Bay			
Class/Order/Family/Species	A	B	C	D	E	F	A	B	C	D	A	B	C	D	E	189G	189S	6	24
Atyidae																			
Haminoea antillarum (Orbigny, 1841)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5578	1418	0	0
Haminoea succinea (Conrad, 1846)	0	0	0	0	189	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Bivalvia																			
Bivalvia (unidentified)	158	142	118	701	0	95	0	0	189	662	0	0	189	189	0	94	0	0	0
Nuculoida																			
Nuculanidae																			
Nuculana acuta (Conrad, 1832)	95	0	95	252	725	0	0	0	0	95	0	95	851	284	252	0	0	0	0
Nuculana concentrica Say,1824	142	284	221	142	95	0	0	0	0	95	0	0	473	0	0	0	0	0	0
Mytiloida																			
Mytilidae																			
Amygdalum papyrium (Conrad, 1846)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	265	95	0	0
Brachidontes exustus (Linné, 1758)	95	95	0	0	0	95	0	378	0	0	0	0	0	0	0	520	95	0	0
Arcoida																			
Arcidae																			
Anadara ovalis (Bruguière, 1789)	0	0	0	95	0	0	0	0	0	0	0	0	0	0	95	0	0	0	0
Ostreoida																			
Ostreidae																			
Crassostrea virginica (Gmelin, 1791)	0	95	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Veneroida																			
Kelliidae																			
Aligena texasiana Harry, 1969	0	0	95	95	0	0	0	0	95	246	0	95	0	605	378	0	0	0	0
Montacutidae																			
Mysella planulata (Stimpson, 1851)	378	142	95	95	0	0	0	0	0	643	0	95	331	0	0	0	0	0	0
Crassatellidae																			
Crassinella lunulata (Conrad, 1834)	0	0	0	0	0	0	0	0	0	0	0	0	189	0	0	0	0	0	0
Cardiidae																			
Laevicardium mortoni (Conrad, 1830)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	126	95	0	0
Mactridae																			
Mactra fragilis Gmelin, 1791	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	359	95	0	0
Mulinia lateralis (Say, 1822)	714	544	1429	260	7162	993	6145	6802	2920	1642	1377	2902	697	1721	615	95	315	352	1150
Rangia cuneata (Sowerby, 1831)	0	0	0	0	0	0	578	142	0	0	0	0	0	0	0	0	0	0	0
Solenidae																			
Ensis minor Dall, 1900	350	0	0	0	0	0	0	95	95	473	0	95	0	0	0	0	0	0	0
Solen viridis Say, 1821	0	0	0	0	0	0	0	0	0	0	0	0	0	189	0	0	0	0	0
Tellinidae																			
Macoma brevifrons (Say, 1834)	0	0	0	0	0	0	0	0	0	0	0	0	0	95	0	0	0	0	0
Macoma mitchelli Dall, 1895	464	228	95	236	189	1059	431	441	244	490	1305	977	95	0	0	0	0	0	0
Macoma tenta (Say, 1834)	0	0	0	95	0	0	0	0	0	95	0	0	189	189	189	0	0	0	0
Tellidora cristata Récluz, 1842	0	0	0	0	0	0	0	0	0	0	0	0	0	0	95	0	0	0	0
Tellina sp.	378	284	0	95	0	0	0	95	0	95	0	0	425	189	378	189	0	0	0
Tellina tampaensis Conrad, 1866	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	95	95	0	0
Tellina texana Dall, 1900	0	0	0	95	0	0	0	0	0	0	0	0	0	0	0	95	95	0	0

(continued)

Table 3. Continued.

	Lavaca-Colorado Estuary						Guadalupe Estuary				Nueces Estuary					Laguna Madre-Baffin Bay			
Class/Order/Family/Species	A	B	C	D	E	F	A	B	C	D	A	B	C	D	E	189G	189S	6	24
Semelidae																			
Abra aequalis (Say, 1822)	0	0	0	176	0	0	0	0	0	0	0	0	95	0	189	0	0	0	0
Solecurtidae																			
Tagelus divisus (Spengler, 1794)	0	0	0	0	0	0	0	0	0	0	0	0	0	284	0	0	0	0	0
Tagelus plebeius (Lightfoot, 1786)	433	0	0	0	0	0	0	0	189	189	0	0	284	0	0	0	0	0	0
Veneridae																			
Anomalocardia auberiana (Orbigny, 1842)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	189	662	0	0
Chione cancellata (Linné, 1767)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	993	165	0	0
Mercenaria campechiensis (Gmelin, 1791)	0	0	0	95	0	0	0	0	95	95	0	0	0	95	0	0	0	0	0
Myoida																			
Myidae																			
Paramya subovata (Conrad, 1845)	0	0	0	700	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Corbulidae																			
Corbula contracta Say, 1822	0	0	0	819	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hiatellidae																			
Hiatella arctica (Linné, 1767)	0	0	0	536	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pholadomyoida																			
Lyonsiidae																			
Lyonsia floridana Conrad, 1849	0	0	95	0	0	0	0	0	95	0	0	189	95	189	0	0	0	0	0
Pandoridae																			
Pandora trilineata Say, 1822	0	95	0	95	0	0	0	0	0	95	0	0	0	0	0	0	0	0	0
Periplomatidae																			
Periploma margaritaceum (Lamarck, 1801)	0	0	425	1182	0	0	0	0	95	0	0	0	0	0	0	0	0	0	0
Periploma orbiculare Guppy, 1878	0	0	378	1179	0	0	0	0	0	315	0	0	268	126	95	0	0	0	0
Scaphopoda																			
Dentaliida																			
Dentaliidae																			
Dentalium texasianum Philippi, 1849	0	0	0	95	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

the seagrass habitats of Laguna Madre, versus the open bay habitats characteristic of Baffin Bay. Stations 189G and 189S were identical, and stations 6 and 24 were identical (Fig. 3D). Gastropods were rich in Laguna Madre (13 species in stations 189G and 11 species in 189S), but few in Baffin Bay (3 species each at stations 6 and 24) (Table 3). Only one bivalve species, *Mulinia lateralis*, was ever found in Baffin Bay. In contrast, 11 species were found in station 189G and 9 species were found in station 189S. Because of the concomitant low numbers of individuals found in Baffin Bay, the proportion of each class was similar. Gastropods dominated this ecosystem, 77% at station 189G, 71% at 189S, 67% at 6, and 38% at 24.

Community characteristics varied among the estuaries as well as within the estuaries (Table 4). Salinity generally increased from north to south. The lowest salinity, open-bay station (Guadalupe A) had the highest abundance and biomass indicating high productivity. The only high-salinity station with high abundance and biomass was the seagrass habitat of Laguna Madre (station 189G). The hypersaline environments of Baffin Bay had the lowest abundances and biomasses. Diversity was generally highest near Gulf passes and in the seagrass habitats. Overall, these Texas estuaries had a mean of 14 species of small infaunal mollusks, with a mean abundance of 7,500 individuals/m^2, and mean biomass of 2.4 g/m^2.

Table 4. Summary of zoogeographic distributions and estuarine characteristics: mean salinity (psu), number of species, abundance (N/m^2), and biomass (g/m^2) for each station over the entire study period.

Estuary	Station	Salinity	Species	Abundance	Biomass
Lavaca-Colorado	A	15	18	4,700	1.13
	B	19	18	3,800	0.40
	C	24	18	4,000	0.40
	D	29	26	8,100	1.99
	E	22	10	9,700	1.38
	F	17	8	2,800	2.02
Guadalupe	A	7	8	35,000	5.93
	B	11	11	13,600	2.95
	C	15	17	9,700	1.65
	D	16	23	7,400	8.43
Nueces	A	23	4	2,900	1.05
	B	27	9	4,800	2.61
	C	31	8	5,000	0.92
	D	32	22	7,200	0.55
	E	28	15	3,500	0.77
Laguna Madre	189G	38	24	13,000	10.41
	189S	38	20	5,000	1.34
Baffin Bay	6	40	4	1,900	0.25
	24	42	4	1,100	1.00

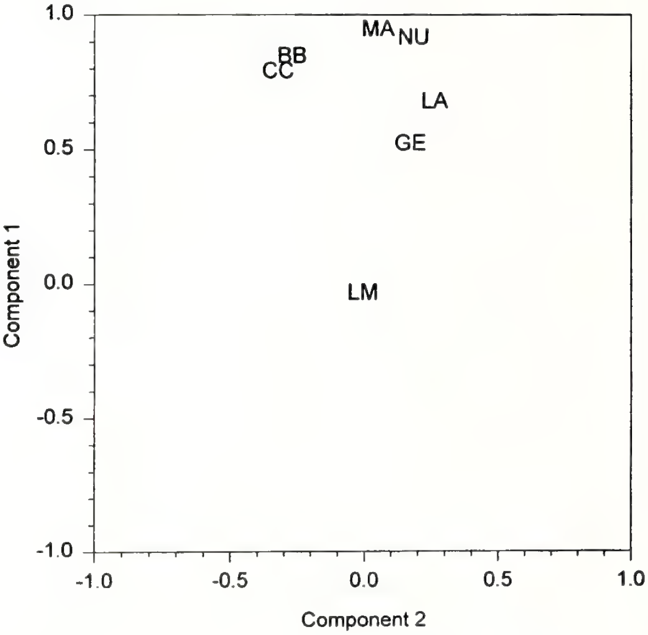

Fig 4. Principal components analysis of molluscan communities in each bay over the entire study period. (BB = Baffin Bay; CC = Corpus Christi Bay; GE = Guadalupe Estuary (San Antonio Bay); LA = Lavaca Bay; LM = Laguna Madre; MA = Matagorda Bay; NU = Nueces Bay).

Each estuary is generally composed of two bays, except for the Guadalupe Estuary (Fig. 1). The seagrass-dominated, hypersaline Laguna Madre was very different from all the open-bay habitats in terms of species composition (Fig. 4). The two secondary bays that receive the most freshwater inflow (Lavaca and San Antonio Bays) were alike and shared a similar space in the PCA diagram (Fig. 4). The restricted freshwater inflow into Nueces Bay caused that community to appear more like a primary bay community than a secondary bay community. The two most-saline bays in south Texas (Corpus Christi and Baffin Bays) were alike. In general, the first PCA axis is separating communities on a gradient from seagrass to fresh to saline habitats. The second PCA axis appears to be separating large open bays from smaller closed bays.

The infaunal molluscan community in Texas estuaries was dominated by the dwarf surf clam, *Mulinia lateralis* (Table 5). *M. lateralis* populations were more abundant in the more freshwater bays of the northern part of the study area. Only in Laguna Madre, which is dominated by seagrass beds, were other species found to dominate. Salinity alone is not the only factor determining mollusk distributions or dominance. Estuarine physiography is also very important. For example, *M. lateralis* was found in Lavaca Bay and Matagorda Bay, but was at highest density in stations C and E, which have moderate inflow influence, and

Table 5. Dominant species in each estuary, with overall mean abundance (N/m²) in parentheses.

Estuary	1st Dominant	2nd Dominant	3rd Dominant
Lavaca-Colorado	*Mulinia lateralis* (1900)	*Macoma mitchelli* (400)	*Acteocina canaliculata* (400)
Guadalupe	*Texadina sphinctostoma* (6400)	*Mulinia lateralis* (4400)	*Macoma mitchelli* (400)
Nueces	*Mulinia lateralis* (150)	*Macoma mitchelli* (50)	*Rictaxis punctostriatus* (300)
Laguna Madre	*Haminoea antillarum* (400)	*Caecum pulchellum* (500)	*Chione cancellata* (600)
Baffin Bay	*Mulinia lateralis* (800)	*Rictaxis punctostriatus* (500)	*Acteocina canaliculata* (100)

moderate mean salinities near 23 psu (Table 3). But, in the higher-salinity Baffin Bay (about 41 psu), it was still the dominant species (Table 3). *M. lateralis* was abundant in the Guadalupe Estuary where salinities ranged from 7-16 psu, but was most abundant in stations A and B where the salinity was low, about 9 psu (Table 3). *M. lateralis* was also equally present in most stations in the Nueces Estuary, where mean salinities ranged from 23 to 32 psu (Table 3). On average, *M. lateralis* was more dense in the secondary bays than in the primary bays from San Antonio Bay south to Baffin Bay. The only exception was in Matagorda Bay, but here it also occurred nearer the freshwater inflow sources, and was rare near the Gulf pass.

There was a great deal of temporal variability with respect to the densities of all these organisms. However, this was most exemplified by *Mulinia lateralis* (Fig. 5). The temporal patterns within estuaries were similar, but of different magnitude. The periods between 1987-1988 and 1992-1993 were good years for *M. lateralis* in the central estuaries (Fig. 5A). This pattern was not as distinct in the southern estuaries (Fig. 5B). The good years corresponded to wet years which followed, or occurred during El Niño events. *M. lateralis* practically disappeared from Baffin Bay during 1990-1992 corresponding to the occurrence of a severe brown-tide bloom. Large-scale climatic events seem to be controlling *M. lateralis* populations.

DISCUSSION

On one hand, there appears to be a typical, open-bay, "Texas molluscan" community. The community is dominated by small bivalves. Typically the small bivalves represent two-thirds of the community. The dominant species are *Mulinia lateralis* and *Macoma mitchelli*. The estuarine-wide pattern is influenced by the patterns near the river mouth, where bivalves can be as high as 90% of the population. The dominance of these clams is important to the entire trophic structure of Texas estuaries, because *M. lateralis* is the predominant food source for black drum, *Pogonias cromis* (Goode, 1884) (fide Martin, 1979).

There are two exceptions to this "generalized Texas community," where gastropods are dominant: San Antonio Bay and Laguna Madre. Laguna Madre is dominated by seagrass-bed habitats, and diversity and standing stocks are generally very high. This is a direct result of the value of the seagrass habitats. San Antonio Bay is unusual in that it is dominated by freshwater inflow. This is due to high turnover rates of water and low rates of marine exchange. It appears that hydrography and physiography are responsible for the different kind of community found in San Antonio Bay.

During the entire study period, except for 1989, there was a continuous brown-tide bloom in Laguna Madre and Baffin Bay (Stockwell *et al.*, 1993). Other brown-tide blooms have had catastrophic effects on bivalves (Shumway, 1990). Effects have ranged from reproductive or recruitment failures (Bricelj *et al.*, 1987; Tracey, 1988), to adverse effects on feeding (Tracey, 1988; Tracey *et al.*, 1988; Bricelj and Kuenstner, 1989), to a toxic effect (Draper *et al.*, 1989; Tracey *et al.*, 1990; Gainey and Shumway, 1991). So, it is possible that the trend reported here is not normal, and could be due to the effects of a brown tide. We know that *Mulinia lateralis* feeds on the organisms that produce brown tide (Montagna *et al.*, 1993), so it is likely that the changes in Baffin Bay are related to an effect on larvae, reproduction, or are completely unrelated to brown tide. If the brown tide has had an effect on bivalves in Laguna Madre, then the conclusion that gastropods dominate in the Laguna is not a generality, but sim-

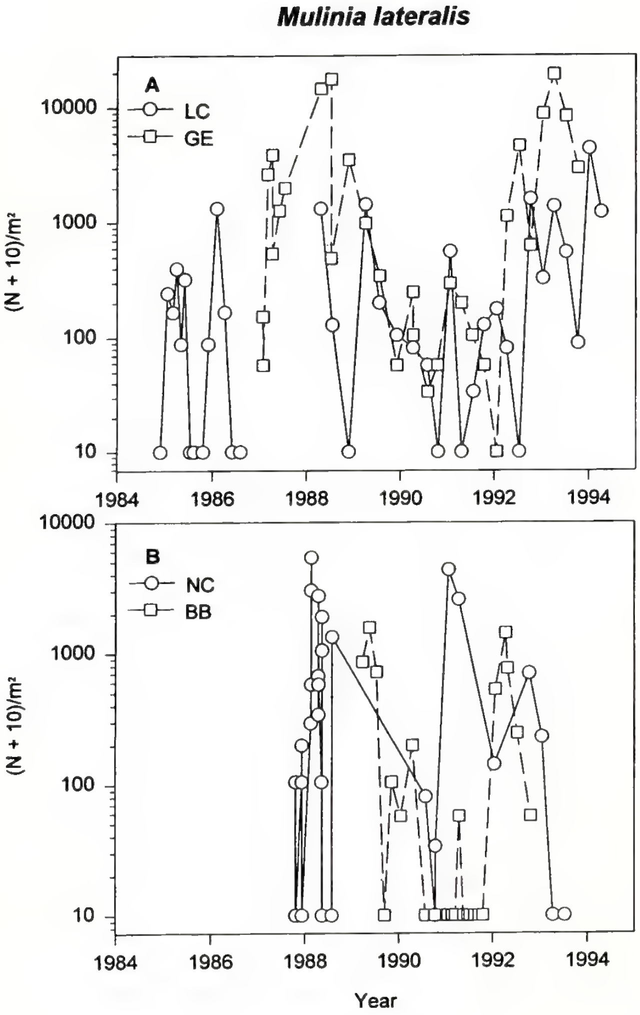

Fig 5. *Mulinia lateralis*, average population abundance over entire estuary at each study period. A. In the Lavaca-Colorado (LC) and Guadalupe (GE) Estuaries. B. In the Nueces Estuary (NC) and Baffin Bay (BB).

ply a temporary event caused by the brown tide.

Brown tide is not a possible explanation of the dominance by gastropods in San Antonio Bay. In fact, San Antonio Bay has a large population of *Mulinia lateralis* (Fig. 5). It is merely that the population of *Texadina sphinctostoma* is enormous at the mouth of the Guadalupe River (Table 3). The unidentified gastropods in these samples are all very small juveniles, and are also likely to be *T. sphinctostoma*. San Antonio Bay is also less like other Texas bays in terms of physiography. The demarcation between the primary and secondary bay is less distinct (Fig. 1), and there is very indirect exchange between the bay and the Gulf of Mexico. In San Antonio Bay most living freshwater species are found in the upper bay and along the western shoreline, being conspicuously absent from the eastern shore (Parker, 1959). The distribution of *Rangia cuneata* in upper San Antonio Bay and along the western shoreline conforms with the dominant freshwater flow pattern (Ladd, 1951). In general, the average pattern in the Guadalupe Estuary is masked by an unusual pattern of freshwater species near the river and the circulation pattern.

Ecological studies over the years have demonstrated the importance of salinity as a factor in affecting the distribution of marine and estuarine organisms. The number of species, but not necessarily the observed total biomass, increases as one proceeds along a salinity gradient from the freshwater side of a large estuary to the open sea (Springer and Woodburn, 1960; Gunter, 1961). This trend is also evident among Texas Mollusca (Table 4). The dominant species found in the current study are *Mulinia lateralis* and *Texadina sphinctostoma* (Table 3). The distribution of these species is strongly linked to long-term environmental conditions, although responses to flood conditions may result in rapid population changes.

Texadina sphinctostoma populations increase following peaks in freshwater inflow (Harper, 1973; Matthews *et al.*, 1974). This is apparently a breeding response caused by a salinity decline (Harper, 1973). *T. sphinctostoma* carries its eggs on the shell and undergoes direct development with the young ready to assume adult existence upon emerging from the egg. *T. sphinctostoma* is commonly reported as one of the most dominant gastropod inhabitants of the river-influenced upper bays of the Texas coast (Ladd, 1951; Ladd *et al.*, 1957; Parker, 1959; Harper, 1973; Matthews *et al.*, 1974; Gilmore *et al.*, 1976; White *et al.*, 1983, 1989; Staff *et al.*, 1985).

Mulinia lateralis is an extremely hardy species, ranging from Prince Edward Island, Canada, to Yucatan, Mexico, and in salinities from 5 to 80 ppt (Parker, 1975). It is an opportunist of adversity because it can colonize rapidly after a disturbance event such as dredging or heavy rain (Flint *et al.*, 1981; Flint and Younk, 1983). It is one of the more abundant mollusks in the low-salinity bay heads of the Gulf coast (Hopkins *et al.*, 1973). In San Antonio Bay, Matthews *et al.* (1974) and Harper (1973) reported *M. lateralis* widely distributed from brackish water to higher salinity as found here. Both reports indicated that the close resemblance of *Rangia cuneata* juveniles and *M. lateralis* may have resulted in numerous misidentifications at the low salinity stations. In Laguna Madre (Alazan Bay) *M. lateralis* was the most abundant and widespread mollusk (Martin, 1979; Cornelius, 1984). *M. lateralis* is widely reported from other bays around the Gulf and Atlantic coasts of the U.S. Spawning was observed in the Tred Avon River, Maryland, and Chesapeake Bay where it was observed to have a continuous period of setting from a single spawning cycle from May through November (Shaw, 1965; Holland *et al.*, 1977). In Alazan Bay, Texas, Cornelius (1984) observed juveniles in all months except December, and Poff (1973) observed year-round spawning in Trinity Bay, Texas. *M. lateralis* has a very short generation time and is capable of successfully spawning at 3 mm in length which is approximately 60 days old (Calabrese, 1969a). Embryo survival and development for *M. lateralis*, as it is with *R. cuneata*, is dependent on certain salinity and temperature ranges. *M. lateralis* developed into normal larvae throughout the salinity range of 15 to 35 ppt and the temperature range of 10 to 30°C (Calabrese, 1969b). This clam is an important food item to bottom feeding organisms, *i.e.* the black drum (Pearson, 1929; Breuer, 1957; Simmons and Breuer, 1962; Martin, 1979) and to the greater and lesser scaup ducks [*Aythya marila nearctica* Stejneger, 1885, and *A. affinis* (Eyton, 1838), respectively] (Cronan, 1957). Large rafts of scaup ducks were observed in upper San Antonio Bay in November 1988 corresponding to high densities of *M. lateralis* (pers. obs.).

Humans have had an enormous impact on coastal ecosystems in general, and Texas is no exception. Recently, intervention has been attempted by State agencies to try and conserve or enhance natural resources. Two projects occurred during the current study: a mandated freshwater release schedule in Nueces Bay, and a diversion of the Colorado River to the east arm of Matagorda Bay. Both projects appear to have had a desirable effect, if this is defined as enhanced molluscan communities. The physical effect of both projects is obvious from the lowered salinity values that have occurred (Fig. 2, Table 4). In the Nueces Estuary, the stations A and B had very high salinities, and no longer exhibit this characteristic. There were generally low abundances and diversity prior to the mandated releases, and there is now a productive community. In the Lavaca-Colorado Estuary, station F is now very much like station A in terms of salinity and species composition. Both projects appear to have had the desired effects. However, there are two caveats. The changes that occurred in the Nueces Estuary coincided with an El Niño event, and therefore may have occurred without the releases. The changes that occurred in the Lavaca-Colorado Estuary are also being mitigated by siltation, which threatens to close the diversion or restrict freshwater inflow. Only after several more years of sampling, to determine the long-term effect, can we be certain that these two projects will have lasting value.

Freshwater inflow has obvious benefits to estuaries. Only Texas estuaries with high freshwater inflow rates support a productive shellfish industry (Table 1). The distribution and abundance of *Mulinia lateralis* demonstrates the importance of inflow and the physical characteristics of estuaries. The variability of salinity patterns is more important than the absolute salinity values. *M. lateralis* occurs most frequently in Baffin Bay, which is hypersaline, and Lavaca Bay and San Antonio Bay, which are both low-salinity regions. However, all three bays are secondary bays. This means that freshets have large impacts on these systems, and salinity values change rapidly. If only absolute values of salinity were important, then these patterns would not exist. It is more likely that recruitment events for *M. lateralis* are initiated by a large change in the salinity value, which predominantly occurs in secondary bays. *M. lateralis* is apparently a good indicator species of freshwater inflow effects.

In the present study, we have concentrated on the effects of physical factors, *e.g.* freshwater inflow, estuarine physiography, and time. Obviously, biological interactions are also occurring. However, we have little information to determine how to separate effects due to physical factors and biological interactions, *e.g.* competition and predation.

There are obviously interactions among three geophysical factors which regulate and control the structure and function of molluscan communities in Texas estuaries. These factors are climate (which regulates rates of freshwater inflow), estuarine physiography (which regulates circulation patterns and the degree of marine exchange), and the presence of specific habitats (particularly seagrass beds). These factors control the landscape of the estuary and this determines both the makeup and productivity of the molluscan community. Climate and physiography interact to control the salinity patterns among and within the estuaries. The salinity patterns are good surrogates for indicating the effects of climate and physiography, but salinity itself is not the controlling factor. It is clear that freshwater inflow is very important in maintaining estuarine productivity. The potential for enhancing marine resources by water management projects appears to be a fruitful endeavor, but this must be confirmed with long-term ecosystem-level research.

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The hypobranchial gland of the estuarine snail *Stramonita haemastoma canaliculata* (Gray) (Prosobranchia: Muricidae): a light and electron microscopical study

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Abstract. The general structure and secretory features of the hypobranchial gland of *Stramonita haemastoma canaliculata* (Gray, 1839) were investigated using light microscopy (LM), scanning electron microscopy (SEM), and transmission electron microscopy (TEM). The gland is composed of three distinct regions and occupies the right medial and lateral portions of the dorsal mantle tissue. The ctenidia, osphradium, and rectum occupy the remainder of the mantle cavity. Eight distinct cell types were identified by LM. SEM and TEM analysis revealed active secretory cells in the two lateral areas (regions I and III). The ventral surface of these regions is ciliated and possesses pores through which the secretory product is released into the mantle cavity. Region II apparently functions as a temporary storage area where secretory products accumulate prior to their release from the snail. One of the secretory products of the hypobranchial gland possesses the staining characteristics of the "Tyrian Purple" dye. Its functional role in the feeding process of the snail, if any, is presently unknown.

The southern oyster drill *Stramonita (= Thais) haemastoma canaliculata* (Gray, 1839) (Abbott, 1974; Kool, 1986, 1987) is a muricid prosobranch inhabiting estuarine environments along the Louisiana gulf coast. This species is the primary predator on the eastern oyster *Crassostrea virginica* (Gmelin, 1791) and is believed to represent the greatest hazard to the survival of *C. virginica* in this region (Pollard, 1973). This predation results in the snail being an economically important destructive agent to oyster fisheries along the gulf coast (St. Amant, 1938, 1957; Burkenroad, 1931; Roller and Stickle, 1988, 1989). The oyster drill has also been observed to feed on barnacles in the field and on *Rangia cuneata* (Sowerby, 1831) in the laboratory (Roller and Stickle, 1984; Brown and Richardson, 1987). Predation of *S. haemastoma canaliculata* on oysters and the regenerative ability of its feeding apparatus, as well as its adaptation to low salinity environments, have been previously described (Garton and Stickle, 1980; Roller *et al.*, 1984; Brown and Richardson, 1987; Roller and Stickle, 1988, 1989).

Muricid gastropods possess several structures that allow predation on barnacles, bivalves, and other gastropods (Fretter and Graham, 1962; Webb and Saleuddin, 1977; Carriker, 1981; Roller *et al.*, 1984). These structures include: (1) the radula, a chitinous ribbon of teeth located in the proboscis; (2) the accessory boring organ, a glandular structure located in the foot which produces a secretion that assists in the shell-boring process; (3) the salivary glands in the buccal cavity; and presumably (4) the hypobranchial gland, a component of the dorsal mantle. The radula and accessory boring organ are used to bore holes in the margin of the prey's shell (in the case of bivalves) after which, a paralytic toxin is presumably introduced into the mantle cavity, immobilizing the prey by paralyzing the adductor muscles (Carriker, 1981). The drill then wedges the lip of its shell between the gaped valves of the prey and opens it further, exposing the soft flesh for consumption. The structure and functions of the radula, accessory boring organ, and salivary glands for several species of muricids have been previously documented (Fretter and Graham, 1962; Carriker, 1981; Huang and Mir, 1972; Prezant, 1983; Roller *et al.*, 1984). The hypobranchial gland of muricids, and the color change of its pigmented secretion has been studied to a lesser extent, and most of these investigations have involved primarily histochemical and/or biochemical analyses (Keyl *et al.*, 1957; Whittaker, 1960; Hyman, 1967; Roseghini *et al.*, 1970; Huang and Mir, 1971, 1972;

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Roseghini, 1971; Ottaviani, 1978; Bolognani-Fantin and Ottaviani, 1981; Srilakshmi, 1991; Michel *et al.*, 1992). However, there is a paucity of data on the hypobranchial gland of *Stramonita haemastoma canaliculata*, and no previous investigation has included electron microscopy as an analytical tool.

The objectives of the present investigation were to: (1) examine the general morphological features of the hypobranchial gland of *Stramonita haemastoma canaliculata* using stereo-dissection and compound light microscopy; (2) determine anatomical relationships of the gland to other structures located in the mantle cavity as well as to other feeding structures located in the buccal mass; (3) examine the ventral surface of the gland using scanning electron microscopy (SEM) to elucidate the mechanism for release of the secretion; (4) use transmission electron microscopy (TEM) to examine intracellular features of the gland; and (5) examine the color change of the hypobranchial secretion (Tyrian Purple) once released by the snail.

MATERIALS AND METHODS

COLLECTION AND MAINTENANCE OF SNAILS

Fifty-seven adult oyster drills (shell length = 54.6 ± 7.6 mm) were collected in the vicinity of Caminada Pass, Grand Isle, Louisiana, U. S. A. (29°12' N; 90°03' W) (Fig. 1) over a four-year period (1990-1994) for this study. The snails were transported within 6 h to the laboratory and placed into 38 l aquaria (10 snails/aquarium) at room temperature (24° ± 1.5°C) and 25 ppt salinity (Instant Ocean® artificial seawater mix). All aquaria were aerated throughout the experiment. Oysters *(Crassostrea virginica)* and clams *(Rangia cuneata)* were provided as prey.

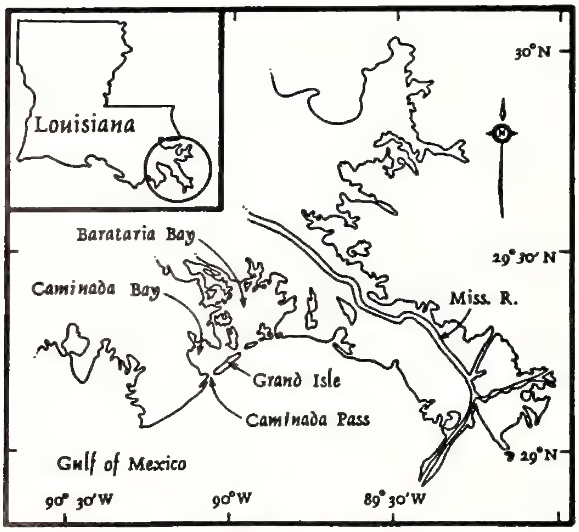


Fig. 1. Map of Louisiana with inset of southeastern coast showing collection site at Caminada Pass.

PREPARATION OF TISSUE

Individual snails were removed from the aquarium, and the shells were blotted dry. Shells were opened by cracking with a hammer at the juncture of the primary body whorl and the spire (Figs. 2a, 4). The visceral mass and dorsal mantle were removed from the shell fragments by severing the columellar muscle with a razor blade. This technique allowed for successful, intact removal of all of the soft body parts with the exception of the terminal portion of the gonad/digestive gland located in the posterior of the spire. Even though the hypobranchial gland is located in the dorsal mantle immediately below the shell, little damage occurred to the tissue in 90% of the specimens. Snails which exhibited any damage to the mantle (*i.e.* torn tissues) were discarded. The soft tissues were immediately dipped into a beaker containing 25 ppt salinity seawater to rinse off small shell debris. To reduce osmotic stress the tissue was kept immersed in seawater during the subsequent dissection procedures. The dorsal mantle, containing the hypobranchial gland, gills, and osphradium, was then removed intact from the visceral mass by severing its lateral margins at the attachment of the columellar muscle (Figs. 2a, 4).

For light microscopy, the mantle tissue was pinned with the ventral surface facing up into a petri dish lined with dental wax and containing fixative (Figs. 3-5). The tissues were allowed to fix overnight. Several fixatives were found suitable (based on cell penetration and osmotic stability): formalin-acetic acid-alcohol (FAA), buffered formalin, and Bouin's Fixative (Humason, 1972). During the fixation process an Olympus® SZH stereo-dissection microscope with a 35 mm camera was used for gross morphological examination. The tissues were then dehydrated in ethanol, cleared in xylene, and embedded in paraffin. Serial cross-sections (5-7 µm) were stained with haematoxylin/eosin (Humason, 1972) and examined with a Nikon Microphot® FXA compound microscope. Additionally, several specimens with intact visceral masses (*i.e.* the entire snail) (Fig. 3b) were cross-sectioned for light microscopy.

For scanning electron microscopy (SEM), the mantle tissue containing the hypobranchial gland was trimmed to a diameter of 10 mm (to fit onto an SEM stub) and fixed overnight with 2.5% glutaraldehyde in 0.2 M sodium cacodylate-sucrose buffer (731 mOsm; pH = 8.0) (Postek *et al.*, 1980; Wischnitzer, 1981; Flegler *et al.*, 1993). In all snails examined, yellow viscous secretions from the gland were found adhering to its ventral surface. Therefore, a 10% solution of glycerol-seawater (25 ppt salinity) was

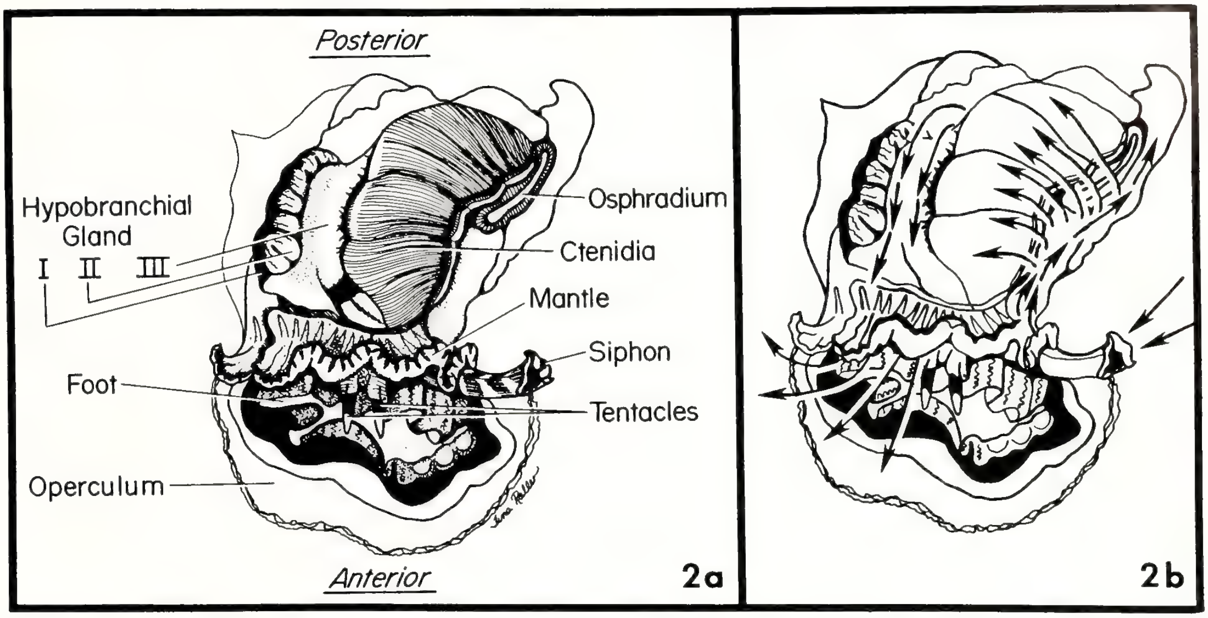


Fig. 2. Diagrams of the dorsal aspect of *Stramonita haemastoma canaliculata* removed from its shell. **(a)** The dorsal mantle has been "cut through" illustrating the mantle cavity structures which are features of the ventral surface. **(b)** The directional flow of seawater through the mantle cavity of the snail.

gently washed over the gland's surface to remove the secretions prior to fixation. After fixation, specimens were rinsed for 30 min in three changes of distilled water to remove all buffer salts, step-wise dehydrated in acetone, critical-point dried in CO_2, mounted on stubs, and sputter-coated with 200 Å of gold-palladium. Surface detail of the mantle tissue was then examined with a Hitachi® S-500 scanning electron microscope at 25 kV.

For transmission electron microscopy (TEM), the three regions of the hypobranchial gland (described in results section) were individually dissected free from the remaining mantle and fixed overnight with 2.5% glutaraldehyde in 0.2 M sodium cacodylate-sucrose buffer (731 mOsm; pH = 8.0) (Postek *et al.*, 1980; Wischnitzer, 1981; Flegler *et al.*, 1993). The tissues were post-fixed for 2 hr in 1% OsO_4 buffered in 0.2 M sodium cacodylate-sucrose (pH = 8.0). Specimens were then dehydrated in ethanol and embedded in a low-viscosity resin (Ted Pella®, Inc.). Ultrathin sections (60-90 nm) were taken using a Sorvall® MT2-B ultramicrotome. Sections were collected on copper grids, contrasted with uranyl acetate-lead citrate, and examined with Hitachi® HU-11A and JEOL® 100-CX transmission electron microscopes at 80 kV.

To visualize the hypobranchial pigment color change (Fig. 6), secretions from four snails (approximately 0.5 ml total) were removed by pipet in a photographic darkroom under safelight and vortexed in 3 ml of seawater. The resulting mixture was pipetted into a vial, photographed (Fig. 7), and then illuminated with a fiber-optic light source to stimulate the color change. The mixture was aerated to enhance the photo-oxidative reaction (Hoffmann, 1990; Michel *et al.*, 1992). The vial was examined and photographed at 15 min intervals over a 2 hr period.

RESULTS

The hypobranchial gland of *Stramonita haemastoma canaliculata* is an anteroposteriorly elongated structure located in the dorsal mantle, lying over the buccal mass (Figs. 2-3). The gland occupies the right medial and lateral sides of the mantle cavity surrounding the rectum on its ventral surface. When dissected and viewed from the ventral aspect (Fig. 3a), three distinct regions of the hypobranchial gland can be discerned (based on location): a lateral portion (we label as region I) surrounding the ventral surface of the rectum on the right side of the body; a medial depression (region II) located adjacent to region I; and a third area (region III) adjacent to region II and medial to the ctenidia (Figs. 3b, 4-5). The ctenidia and osphradium are also mantle derivatives and occupy the left side of the mantle cavity. When viewed from the dorsal aspect, only region II is easily identifiable as a dark pigmented area (Figs. 2a, 4). The ventral surface of region II, in all snails examined, was completely covered by a thick viscous secretion which was bright yellow in color (Fig. 5a). Within 1-2 hr after dissection this secretion changed to a deep purple color (Figs.

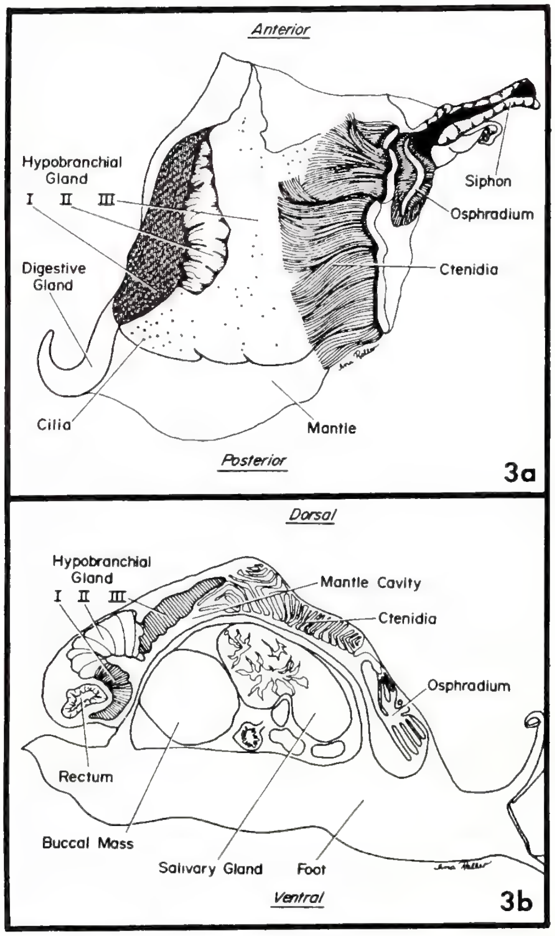


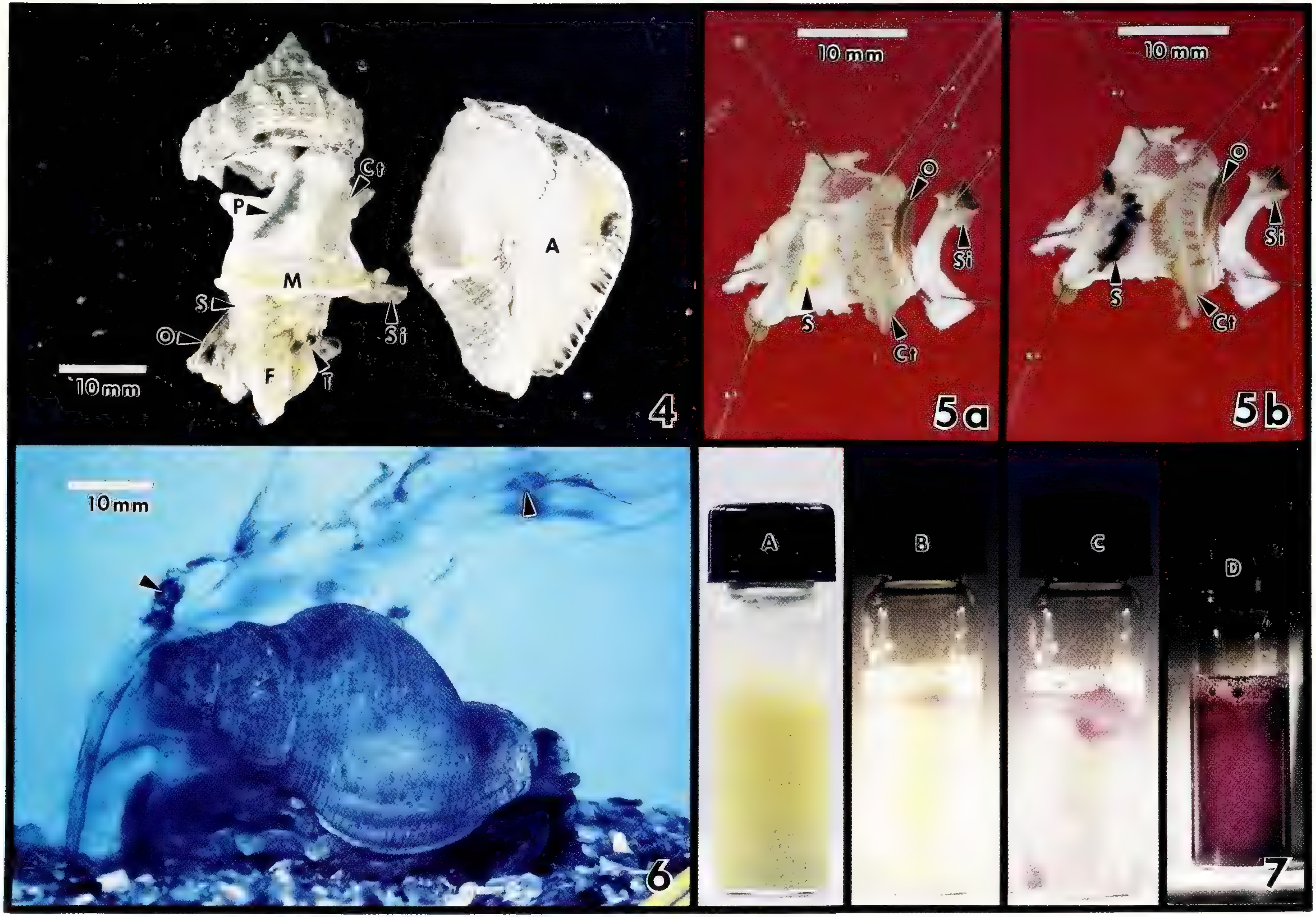
Fig. 3. **(a)** Diagram of ventral surface of the mantle tissue of *Stramonita haemastoma canaliculata* after dissection and removal from visceral mass. This diagram illustrates the three regions of the hypobranchial gland. **(b)** Diagram of a "typical" cross-section through the mantle, mantle cavity, visceral mass, and foot of *Stramonita haemastoma canaliculata*.

5b, 6, 7a-d). Once the secretion had undergone the color change it gave off a foul, pungent odor which would linger on the tissues for days. Even when the secretions were mixed with seawater the odor remained pungent. This secretion was not found on the ventral surface of the other two regions of the hypobranchial gland in any snail examined.

When examined from a cross-sectional, histological aspect (Figs. 8-10, 13-20) the three regions of the hypobranchial gland are more distinct. Region I envelops the ventro-medial surface of the rectum and extends posteriorly for the length of the mantle. Region III is also elongated posteriorly for the length of the mantle and extends dorsomedially to the ctenidia, which with the osphradium, occupy most of the left side of the mantle cavity (Figs. 8-10). However, the anteriormost margin of the mantle (1-2 mm) contains no portion of the hypobranchial gland and forms an anterior mantle lip which extends over the tentacles and is observed in both the living and preserved state (Figs. 2a, 3a, 4). The siphon is a derivative of the anterolateral region on the left side of the mantle lip (Figs. 2-4). Region II of the hypobranchial gland appears more diffuse and stains less eosinophilic in histological sections than the other two regions. In addition, this area does not extend the length of the mantle and thus forms an oval depression between regions I and III (Figs. 8-11). Region II, from histological sections, SEM, and gross dissection (Figs. 5, 10-12), appears to serve primarily for the accumulation of the secretory product prior to release. In all sections examined, no connection was observed between any part of the hypobranchial gland and the rectum or between the gland and the buccal mass which is located directly ventral to the mantle cavity and dorsal to the foot (Figs. 8-9). This observation and the presence of the viscous substance on the ventral surface of the gland (Fig. 5) suggests a specialized path of secretory release for the hypobranchial secretions.

Both regions I and III stain eosinophilic, contain many mucocytes, and appear to be active secretory areas (Figs. 9, 13). Eight distinct cell types were observed randomly distributed in histological sections: empty cells (devoid of secretion) (Fig. 13), large-granule containing cells (Figs. 14-16), large cells with homogeneous cytoplasm (Fig. 16), mucocytes (Figs. 15-19), small-granule containing cells (Fig. 18), ciliated cells (Fig. 18), dark-staining basophilic cells (Fig. 19), and small non-granulated eosinophilic cells (Fig. 19). Both the large-granule containing cells and the small-granule containing cells stained eosinophilic in histological section. Distinct pores were also observed in histological sections (Figs. 14-15). Copious amounts of mucus are released through these pores into the mantle cavity (Fig. 15), with secretory products from the other cell types. The actual product of these other cell types is presently unknown. The empty cells, large cells with homogeneous cytoplasm, and the large-granule cells were tall, cylindrical, and restricted to the epithelium of regions I and III located dorsal to the mantle cavity. Ciliated cells, small-granule cells, and the basophilic cells were observed in both regions I and III epithelia (dorsal to the mantle cavity), as well as in the ventral mantle epithelium (located ventral to the mantle cavity and dorsal to the buccal mass) (Figs. 18-19). The small, eosinophilic cells contained a homogeneous (non-granulated) cytoplasm, and were restricted to the ventral mantle epithelium (Fig. 19). Mucocytes were identified in all epithelia lining the mantle cavity.

An additional group of basophilic cells were observed dorsal to region II and located directly under the shell epithelium (Fig. 20). These cells appeared acinar in their arrangement, suggesting a glandular function; however, they are not located on the secretory epithelium lining



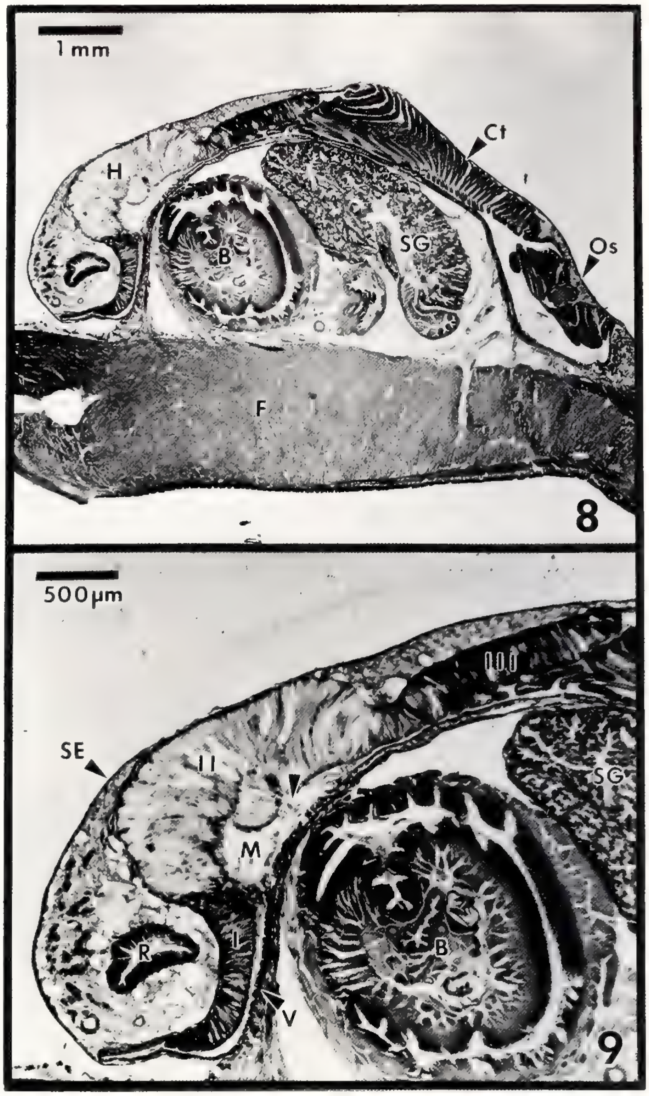
Figs. 4-7. 4. Photograph of the cracked shell and dorsal mantle of *Stramonita haemastoma canaliculata*. (A, aperture; Ct, ctenidia; F, foot; M, mantle; P, pigmented area overlying region II; O, operculum; S, yellow secretory material being released from under anterior margin of mantle; Si, siphon; T, tentacles.) **5(a).** Light micrograph illustrating the ventral surface of a dissected mantle from *S. haemastoma canaliculata*. The yellow viscous secretion is covering region II and has not completely undergone the photo-oxidative color change. (Ct, ctenidia; O, osphradium; S, secretory material in region II; Si, siphon.) **5(b).** Light micrograph illustrating the ventral surface of the dissected mantle after the photo-oxidative reaction has resulted in the purple color of the secretory material. (Ct, ctenidia; O, osphradium; S, secretory material in region II; Si, siphon.) **6.** *S. haemastoma canaliculata* releasing the purple secretion, Tyrian Purple (arrows) while feeding on *Crassostrea virginica*. The snail continually released the secretion over a 1.5 hr period. **7.** Sequence of color change of hypobranchial gland exudate of *S. haemastoma canaliculata*. **A,** immediately after dissection; **B,** 15 min of exposure with a fiber-optic light source; **C,** 30 min of exposure; **D,** 60 min of exposure.

the mantle cavity. They contribute to the dark-staining appearance of region II when viewed from the dorsal aspect in a freshly-dissected specimen (Fig. 4).

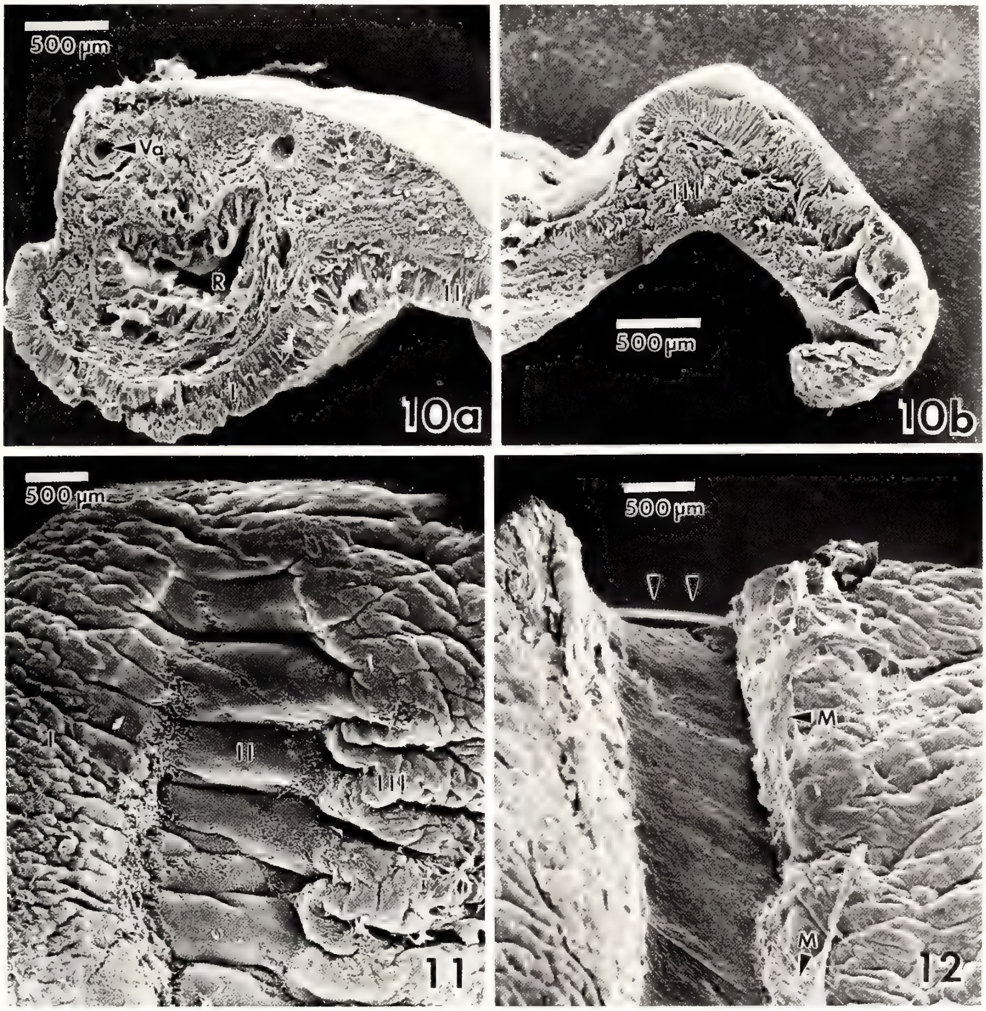
Scanning electron microscopy revealed dense cilia covering the ventral surface of the entire mantle tissue including all three regions of the hypobranchial gland (Figs. 21-26). The actual density of the cilia was impossible to estimate because of their sheer numbers, and because of the extensive mucus secretions adhering to them. The ventral surface of all regions of the gland was uniformly covered with numerous pores through which secretory material was being released (Figs. 21-26). The diameter of pores in regions I and III were 7.8 ± 0.4 and 7.6 ± 0.5 μm (mean ± S.E.) respectively, and there was no significant difference ($P > 0.05$, t-test, $N = 10$ snails) in pore diameter between the two regions (Fig. 27). The secretory product released from a single pore varied in appearance. Some pores contained numerous small, globular "spheres" (Fig. 23), whereas others released long "toothpaste-like" exudates (Figs. 25-26). The latter secretions, when examined under higher magnification, appeared to be composed of smaller spheres approximately 1 μm in diameter (Fig. 26). These spheres correspond in size to the large granules observed with the light microscope (Figs. 13-20). There were no smaller granular-like secretions directly observed with the SEM. There was also no apparent correlation between the type of exudate released and the region of the gland in which it was found; therefore, it is possible that the apparent differences may be due to specimen preparation. However, regardless of the location, all of the secretory products were observed to accumulate in the depression of region II prior to release. In other words, the snail evidently secretes the hypobranchial product directly into the mantle cavity. There was no significant difference ($P > 0.05$, t-test, $N = 10$ snails) in the density of pores between regions I and III (Fig. 28). It was impossible to estimate the pore density opening into region II because this area was covered with mucus secretions that could not be completely removed. Some pores and cilia were observed at the margins of region II; however, it could not be accurately discerned whether or not these were part of region II or the extreme margins of regions I and III.

After release into the mantle cavity, the secretory product appears to be swept out of the cavity under the anterior margin of the mantle by ciliary action. In several of the dissected specimens, some of the hypobranchial secretion was observed being released from under the anterior margin of the mantle (Fig. 4). Additionally, several snails were observed releasing a copious amount of secretion into the seawater while feeding on oysters (Fig. 6).

Transmission electron microscopy revealed hypobranchial cells that exhibited ultrastructural detail characteristic of active secretory cells (Fig. 29a). Secretory activity was indicated by the presence of numerous Golgi, rough endoplasmic reticulum, mitochondria, and distinct electron-dense granules in the cytoplasm. The nuclei of these cells possessed a prominent nucleolus and significant amounts of euchromatin, indicating active transcription of RNA. The electron-dense vesicles of the cytoplasm exhibited a crystalline or granulated composition (Fig. 29b) similar to that seen in vesicles of other organisms (Kilejian, 1974). Numerous secretory vesicles were observed separating from the trans-face or fusing with the cis-face of the Golgi



Figs. 8-9. 8. Light micrograph of a cross-sectional view through the mantle, buccal mass, and foot of *Stramonita haemastoma canaliculata*. (B, buccal mass; Ct, ctenidia; F, foot; H, hypobranchial gland (region II); Os, osphradium; SG, salivary gland.) **9.** Higher magnification of cross-section illustrating regions I, II, and III of the hypobranchial gland of *S. haemastoma canaliculata*. (B, buccal mass; M, mantle cavity; R, rectum; SE, dorsal shell epithelium; SG, salivary gland; V, ventral mantle cavity epithelium.)



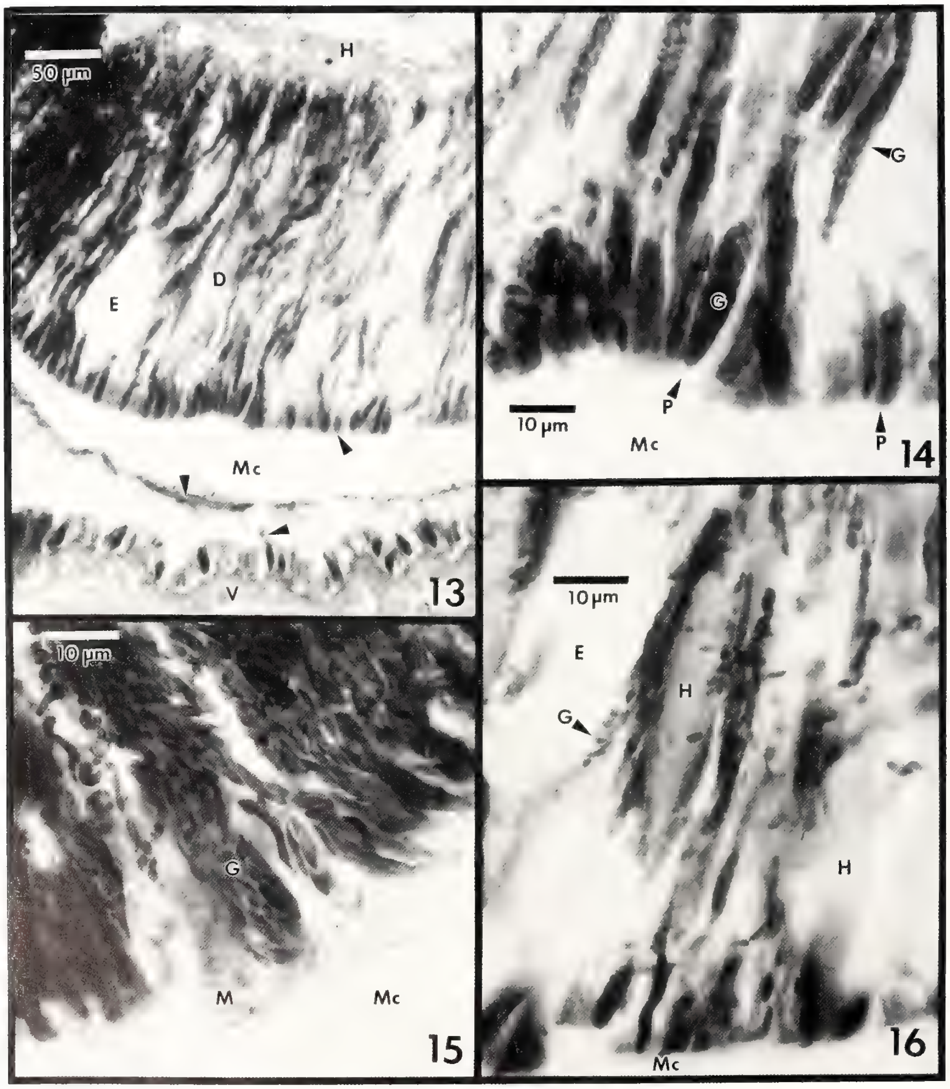
Figs. 10-12. 10(a-b). SEM of two cross-sections of hypobranchial gland through regions I (a), II (a), and III (b). (R, rectum; Va, vas deferens.) **11.** SEM of ventral surface of the hypobranchial gland of *Stramonita haemastoma canaliculata* illustrating the three distinct regions (I, II, and III). **12.** SEM of ventral surface of hypobranchial gland tilted to emphasize the depression (arrows) located in region II. (M, mucus.)

(Fig. 29c) (Stevens and Lowe, 1992; Cormack, 1993; Fawcett, 1994). The fate of these vesicles is unknown; however, it is probable that they may ultimately be released from the cell. TEM also confirmed that the cilia covering the ventral surface of the hypobranchial gland possess the typical 9 x 2 + 2 arrangement of microtubules (Fig. 29d).

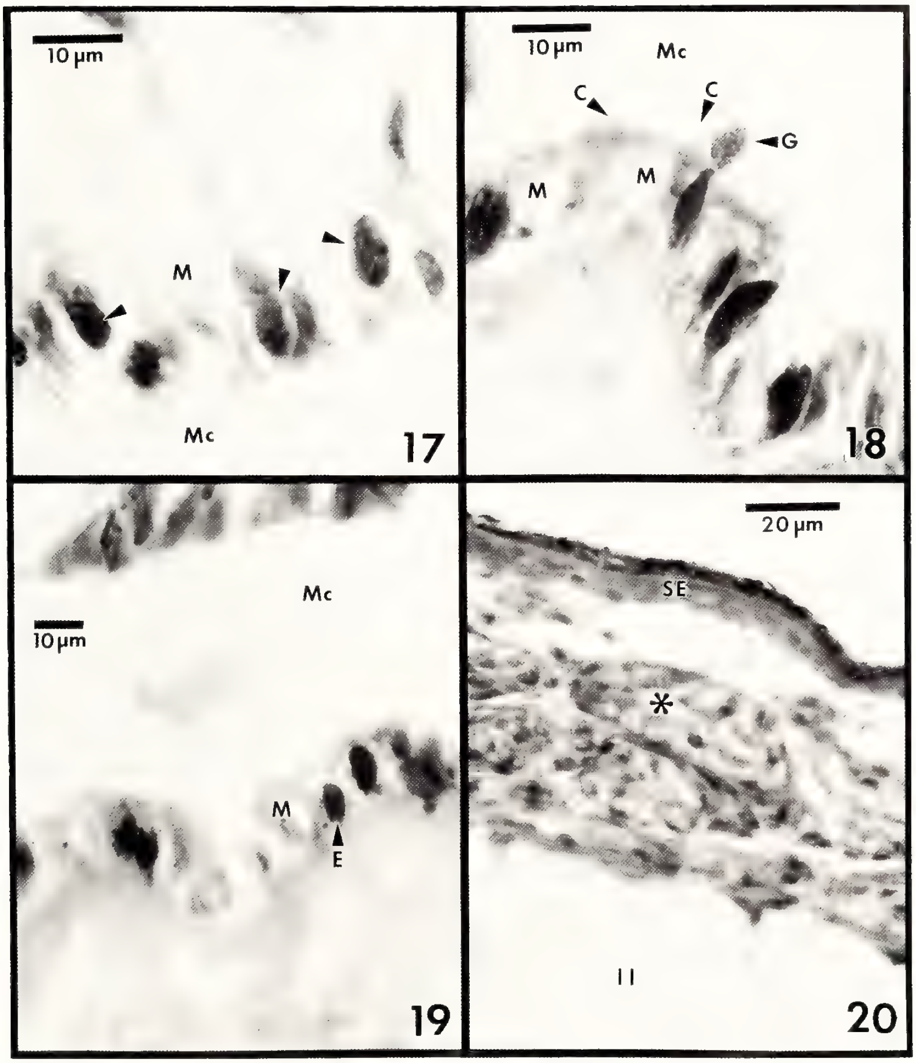
DISCUSSION

The hypobranchial gland of *Stramonita haemastoma canaliculata* is composed of eight distinct types of cells, some of which evidently release secretions through pores directly onto the gland's ciliated ventral surface and thus into the mantle cavity. The cilia create currents responsible for drawing fresh seawater in through the siphon, over the osphradium and ctenidia, across the hypobranchial gland, and out through the anterior margin of the mantle (Fig. 2b). Thick ciliation of osphradial and ctenidial lamellae in this species (Garton *et al.*, 1984) could serve to generate water currents, and thus ventilate the mantle cavity. In addition to assisting olfaction and respiration, this water circulation would also function in the elimination of the hypobranchial secretion and fecal material from the rectum.

Bolognani-Fantin and Ottaviani (1981) used light microscopy and histochemistry to develop a clear concept of the histological organization of the hypobranchial gland in *Murex brandaris* Linné, 1758. They described seven distinct cell types: (1) ciliated cells, (2) empty cells, (3) cells with secretion in big "granula" or irregularly oval-shaped masses, (4) cells with secretion in fine "granula," (5) cells without secretion granula (homogeneous cytoplasm), (6) mucocytes, and (7) "purple-producing" cells. The results of the present investigation reveal similar findings for the hypobranchial gland of *Stramonita haemastoma canaliculata.* The ciliated cells, empty cells, cells containing large granules, cells containing small granules, homogeneous cells, and mucocytes identified in *S. haemastoma canaliculata* are similar to those identified by Bolognani-Fantin and Ottaviani (1981) in *M. brandaris.* It is possible that cells they labeled as "purple-producing" are the same or similar to cells that we have identified as dark-staining basophilic cells; however, they showed no micrographs of these purple-producing cells, and therefore comparison is impossible without further information. We do agree with their suggestion that the empty cells represent cells from which the secretory product had been washed out during histological preparation. Srilakshmi (1991) reported neurosensory cells in the hypobranchial gland of *Morula granulata* (Duclos, 1832). However, his one micrograph illustrated only "gland cells, clear cells, eosinophilic cells, and mucous cells" and no identification of these purported neurosensory cells. Additionally, the micrograph from that study identified a structure that was labeled as the "hypobranchial nerve" located dorsal to the epithelium. The structure in question does not resemble a nerve but rather more closely resembles the dorsal blood vessel containing hemocytes identi-



Figs. 13-16. **13.** Light micrograph of a cross-section of region I of the hypobranchial gland illustrating the dorsal (D) and ventral (V) mantle cavity epithelium, as well as secretory material (arrow) released into mantle cavity (Mc). (E, empty cell; H, hemocytes in blood vessel.) **14.** Light micrograph of region I epithelium illustrating the release of secretory material through pores (P) by large-granulated (G) eosinophilic cells. (Mc, mantle cavity.) **15.** Light micrograph of region III epithelium illustrating the exocytosis of mucus (M) and the release of other secretory material. (G, large-granules released by eosinophilic cells; Mc, mantle cavity.) **16.** Light micrograph of cells with homogeneous cytoplasm (H) from region I epithelium interspersed between large-granulated eosinophilic cells (G). (E, empty cell; Mc, mantle cavity.)

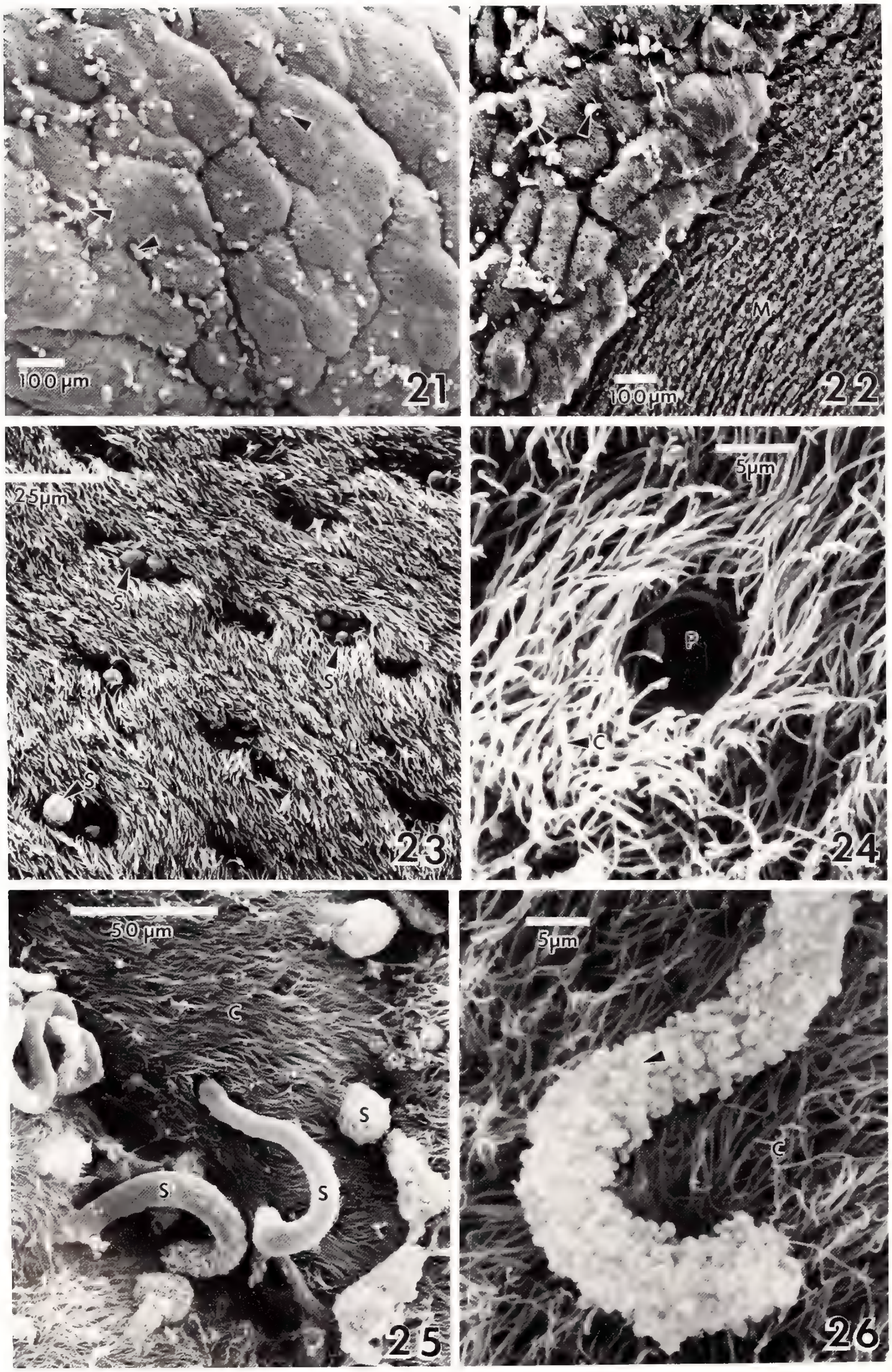


Figs. 17-20. 17. Light micrograph of small basophilic cells from region I epithelium, containing homogeneous material (arrows). (M, mucocyte; Mc, mantle cavity.) **18.** Light micrograph of ventral mantle cavity epithelium illustrating the release of secretory product into the mantle cavity (Mc) by small-granulated (G), eosinophilic cells. (C, ciliated cells; M, mucocytes.) **19.** Light micrograph of small, non-granulated eosinophilic cells (E) of ventral mantle cavity epithelium. (M, mucocyte; Mc, mantle cavity.) **20.** Light micrograph of sectioned dorsal shell epithelium (SE) and dark staining cells (✱) overlying region II. These pigmented cells presumably contribute to the dark coloration overlying region II which can be observed from the dorsal aspect (Fig. 3).

fied in the present study (Fig. 13).

Muricid gastropods are known from antiquity for their production of a brilliant purple pigment, "Tyrian Purple" (6,6'-dibromoindigotin) (Sadler, 1956; Verhecken, 1989, 1990; Hoffmann, 1990; Michel *et al.*, 1992), which was used in the dye process for the robes of Roman royalty and high-ranking officials. The secretions that give rise to this pigment are released by the hypobranchial gland (present investigation) and undergo an enzyme-catalyzed, photo-oxidative reaction (Sadler, 1956; Hoffmann, 1990; Michel *et al.*, 1992) involving the following color change: clear → yellow → green → blue → purple (Verhecken, 1989, 1990). In the present investigation the pigment color change had progressed to a white-yellow phase by the time the snails were dissected, which required only 30-60 sec after the shells were cracked. The remaining color change to a brilliant purple required an additional 30-90 min depending on the light intensity (*i.e.* a fiber-optic light source stimulated fastest color change) (Figs. 7a-d).

St. Amant (1938) identified the hypobranchial gland as the "rectal gland" but stated that the structure was not glandular in appearance. However, he offered no histological evidence of this in his thesis. Later studies (Ottaviani, 1978; Bolognani-Fantin and Ottaviani, 1981; Srilakshmi, 1991; present investigation) have shown that this structure is glandular in nature. Fretter and Graham (1962:23) report-



Figs. 21-26. 21. SEM of ventral surface of region III of the hypobranchial gland of *Stramonita haemastoma canaliculata* illustrating presence of globular secretory material (arrows) on surface. **22.** SEM illustrating the demarcation between the ventral surface of region I of the hypobranchial gland and the posterior mantle surface. (Arrow, secretion being released from pores.) **23.** SEM of the ventral surface of region I of the hypobranchial gland illustrating the dense cilia, and secretion of material (S) through the pores. **24.** SEM of ventral surface of region III of the hypobranchial gland illustrating a prominent pore (P) and dense cilia (C). **25.** SEM illustrating secretion (S) being released from the pores on the ventral surface of the hypobranchial gland (region I). (C, cilia.) **26.** SEM illustrating globular composition (arrow) of secretory material being released from a pore in region III of the hypobranchial gland. (C, cilia.)

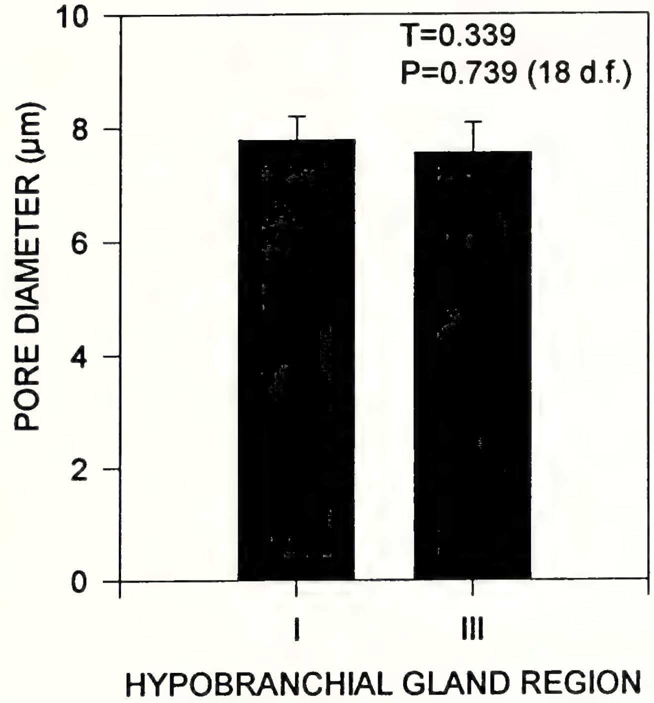


Fig. 27. Pore diameter (µm) (mean ± S.E.) of regions I and III of the hypobranchial gland of *Stramonita haemastoma canaliculata*. There was no significant difference in diameters of pores between the two regions (P > 0.05). (d.f., degrees of freedom; T, t value; P, probability value.)

ed that gastropods and the protobranchiate bivalves are the only two groups of mollusks in which a well-developed hypobranchial gland occurs, and that it functions in the production of a mucus secretion for "trapping and cementing particulate matter sucked into the mantle cavity in the respiratory water current, prior to its expulsion on the right." Secretion of mucoid material by mantle cells is common in many mollusks (Fretter and Graham, 1962; Prezant, 1979), and mucus-producing cells have been identified in the hypobranchial glands of other prosobranchs (Ottaviani, 1978; Bolognani-Fantin and Ottaviani, 1981; Srilakshmi, 1991). It is apparent that this mucus production must, in part, also be an important function of the hypobranchial gland in *Stramonita haemastoma canaliculata* because mucocytes were observed in this study (Figs. 15-19), and copious amounts of clear mucus were observed when the mantle cavity was exposed (Figs. 5, 12). Additionally, the yellow secretion (which gives rise to the Tyrian Purple dye) observed in region II is viscous and presumably composed in part of mucus secretions.

The dark-staining basophilic cells located dorsal to region II (Fig. 20) possibly comprise the rectal gland (Kool, pers. comm.), as they appear glandular in nature; however, we observed no direct connection between these cells and the rectum (Figs. 3b, 8-9). It is possible that the connection was missed in histological sectioning and that the structure is indeed the rectal gland described previously (St. Amant, 1938; Fretter and Graham, 1962).

Previous histochemical and pharmacological investigations attempted to reveal the structure, function, and secretions of the hypobranchial gland in gastropods. Some of these studies reported the release of paralytic substances including physiologically-active choline esters by the hypobranchial glands and salivary glands in several species of muricids (Keyl *et al.*, 1957; Whittaker, 1960; Roseghini *et al.*, 1970; Ottaviani, 1978; Bolognani-Fantin and Ottaviani, 1981; Srilakshmi, 1991) including *Thais (= Stramonita) haemastoma* (Linné, 1767) (Huang and Mir, 1971, 1972; Roseghini, 1971). Presumably, these putative toxins would be used in the feeding process after a snail has drilled a borehole into the shell of its prey (an oyster for example) (Carriker, 1981; Roller *et al.*, 1984). The choline esters would then be released into the mantle cavity of the prey through the borehole, thus paralyzing the adductor muscles, and allowing the snail to wedge the valves of the oyster open, exposing the soft flesh inside. Roseghini (1971) reported the occurrence of large amounts of urocanylcholine (*i.e.* murexine) and imidazolepropionylcholine (dihydromurexine) in the hypobranchial gland of *T.*

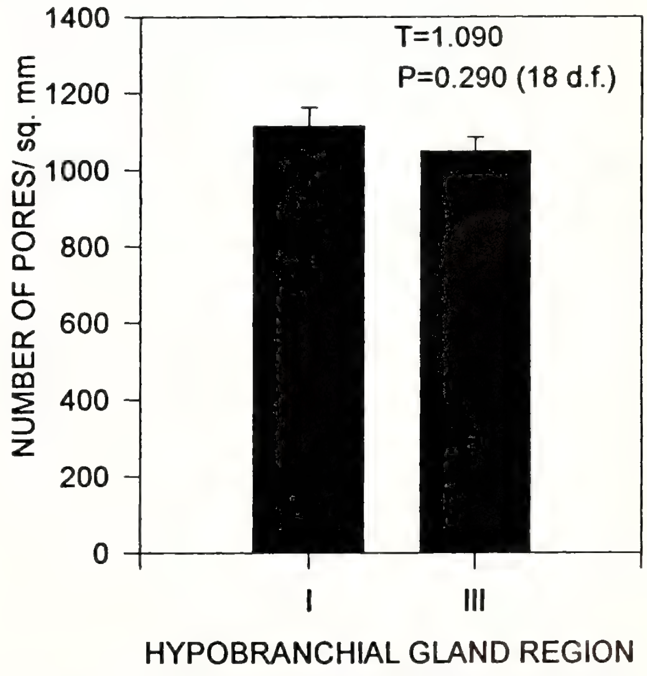


Fig. 28. Pore density (number/mm^2) (mean ± S.E.) of regions I and III of the hypobranchial gland of *Stramonita haemastoma canaliculata*. There was no significant difference in pore density between the two regions (P > 0.05). (d.f., degrees of freedom; T, t value; P, probability value.)

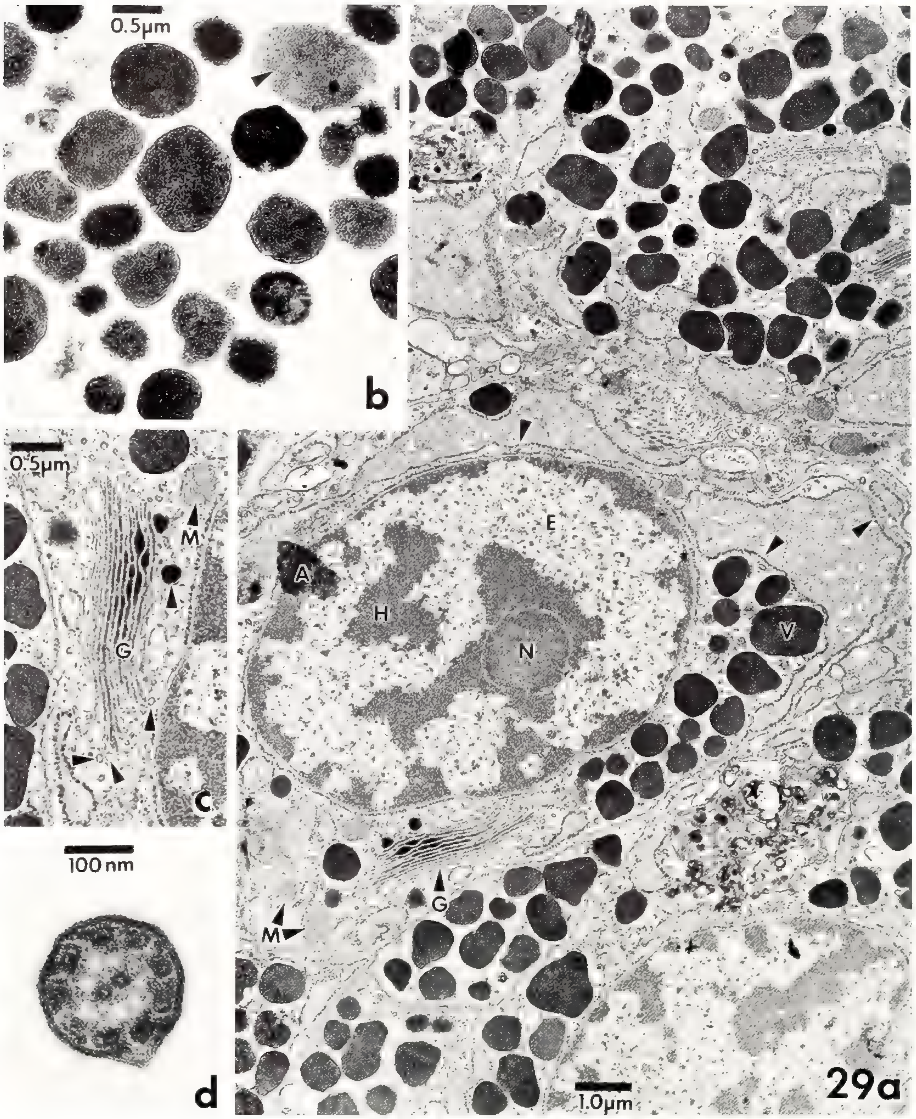


Fig. 29. a. TEM of active secretory cell of region I of the hypobranchial gland of *Stramonita haemastoma canaliculata.* (A, artifact (lead precipitate); E, euchromatin; G, Golgi; H, heterochromatin; M, mitochondria; N, nucleolus; V, electron-dense vesicle; arrows, rough endoplasmic reticulum.) **b.** TEM of secretory vesicles illustrating granular composition (arrow). **c.** TEM illustrating secretory vesicles (arrows) associated with Golgi (G) in the hypobranchial cell of *S. haemastoma canaliculata.* (M, mitochondria.) **d.** TEM of cross-section of cilia on the ventral surface of the hypobranchial gland, illustrating typical 9 x 2 + 2 arrangement of microtubules.

(Purpura) haemastoma. Huang and Mir (1971) examined the pharmacological properties of the hypobranchial gland of *T. haemastoma* and the effect of the secretions on vertebrate tissues. They reported marked increase in blood pressure accompanied by tachycardia in anesthetized cats and an LD_{50} of 215 mg/kg in mice. They also reported increased contractions of various muscle tissues from other mammals. Most predator toxins are specialized for a particular prey species, or group of species. While these previous pharmacological studies provide valuable information, they did not involve the normal prey species of the oyster drill.

In a separate series of experiments we exposed individual bivalves to the combined hypobranchial secretions from four snails with no significant effect relative to untreated controls ($P > 0.05$; $N = 10$). In all instances the bivalves (*Rangia cuneata* and *Crassostrea virginica*) failed to gape appreciably and survived the treatment with no apparent harm. Injection of the hypobranchial extract directly into the mantle cavity of these bivalves (with syringe/needle) likewise had no effect.

Urocanic acid, a histidine derivative, is a precursor to the presumed toxin urocanylcholine (Roseghini *et al.,* 1970). Numerous histidine-rich granules have been previously identified in the malarial parasite *Plasmodium lophurae* Coggeshall, 1938 (Kilejian, 1974), and these granules bear a striking structural resemblance, when examined by TEM, to the larger hypobranchial cell granules identified in the present study. But the apparent lack of toxicity of the hypobranchial secretions from *Stramonita haemastoma canaliculata* on bivalves (present investigation) seems to negate a possible toxin-producing role.

Whether or not the hypobranchial gland functions in toxin production is still unresolved. We suggest that the hypobranchial gland is probably not a "poison gland," based on the following histological evidence: (1) We were unable to find any duct connecting the gland to the buccal mass, salivary glands, or rectum (Figs. 8-9). Such a duct would be conspicuous, having to pass through the mantle cavity to reach either the buccal mass (*i.e.* proboscis) or salivary glands. Therefore, the snail apparently has no way to "inject" the toxin through the borehole and into the mantle cavity of the prey. (2) SEM analysis revealed the presence of pores and dense cilia on the ventral surface of the gland, as well as the actual secretion of material through these pores into the mantle cavity (Figs. 21-26). Therefore, the drill evidently secretes the hypobranchial secretion directly onto "itself" and then flushes it out of the anterior opening into the mantle cavity (again, not an optimal strategy for a poison-producing gland). (3) Snails of this species have been observed to cannibalize each other in our respective laboratories, and one instance of "auto-drilling" has previously been reported (Prezant, 1983). The question of how this toxin affects conspecifics without adversely harming the snail releasing the secretion is still unknown; this fact also makes the hypobranchial gland an unlikely candidate as the producer of the paralytic secretion. Huang and Mir (1972) also questioned the lack of a hypobranchial duct, but offered no histological evidence for any analogous structure. They did report a more pronounced physiological effect of salivary gland extracts from *Thais haemastoma* on cats and mice (LD_{50} = 43 mg/kg) than what they had previously observed (Huang and Mir, 1971) with the hypobranchial extracts. They therefore proposed the salivary gland as a more likely toxin-producing gland. This hypothesis agrees with the present investigation and with reported toxin-producing glands in other species of venomous snails such as *Conus* sp. (Kohn, 1959, Kohn *et al.*, 1960; Songdahl, 1973).

The colored secretion(s) of the hypobranchial gland of *Stramonita haemastoma canaliculata* apparently contains the same or very similar compounds to the Tyrian Purple of antiquity. Modern oyster drills occasionally release this dye when feeding (Fig. 6); however, this has not always been observed during the feeding process and in many instances no trace of the dye was observed during feeding or on the empty bivalve shell. It is doubtful that the dye functions in a similar "visual" manner as the "ink" of cephalopods, because it is rarely released in the copious amounts shown in Fig. 6. It is possible that the function(s) of the hypobranchial secretion can involve an olfactory response during the feeding process. Because the secretions possess such a strong odor after the photo-oxidative reactions are completed, perhaps the secretion masks the "odor" of the prey once it has been opened. Or it could actively repel or deter other opportunistic marine organisms (*e.g.* blue crabs, fish) from dislodging the snail from the oyster and usurping its meal. This would be a highly adaptive strategy for the snail, because it has expended considerable energy opening the prey. Therefore, the function(s) of this dye, and other hypobranchial secretions (*i.e.* choline esters) in predation, and the significance of the dramatic color change are still presently unknown and require further research.

In conclusion, this investigation has revealed the general structure of the hypobranchial gland of *Stramonita haemastoma canaliculata* and has identified the pathway for the release of the secretory product into the mantle cavity of the snail. Based on previous studies and the present investigation, it seems likely that the combined secretion of the hypobranchial gland is composed of several substances each with a potentially distinct function. Further histochemical, biochemical, toxological, and behavioral studies are required to accurately determine the functions of the gland in this species.

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The estuarine clam *Rangia cuneata* (Gray) as a biomonitor of heavy metals under laboratory and field conditions

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Abstract. Accumulation of copper, chromium, cadmium, and lead by *Rangia cuneata* (Gray, 1831) was investigated under laboratory and field conditions. Bioaccumulation rates and concentrations of metals in tissues and the exposure water were determined in the laboratory for calculation of bioconcentration factors (BCF). The BCF ratios ranged between 0 and 422 with significant correlations between exposure time and tissue metal concentration for each metal. Field exposures were conducted below two industrial outfalls that contained some of the metals. High concentrations of the metals were found in the sediments, low concentrations in the water, and intermediate concentrations in the tissues of *R. cuneata*. No significant relationships were found between exposure time and tissue concentrations during the field exposures. However, in most cases a significant increase in tissue burden of the metals occurred after the 40 d exposures, indicating that *R. cuneata* accumulated the most bioavailable forms of the metals under natural conditions. In addition, laboratory-retained clams demonstrated that gametogenesis could be inhibited, thus avoiding seasonal variations in body weight and percent gonadal biomass that affect survival and metal uptake.

Concentrations of toxins in the tissues of aquatic organisms, particularly heavy metals and refractory organic compounds, are widely used to indicate contamination of aquatic systems. This method is especially useful when substances are present intermittently or in very low concentrations. The analysis of water samples will determine the concentration of an analyte only at the time of sampling, whereas bioaccumulators reflect concentrations over a longer time period (Mason, 1991). Bioaccumulators can also bring levels within detection limits of most instruments and operators (National Research Council, 1980).

The use of bivalves as biomonitors of contaminants in aquatic systems is well documented, *e.g.* Ellis, 1937; Bedford *et al.*, 1968; Mathis and Cummings, 1973; Lord *et al.*, 1975; Phillips, 1976, 1977; Manly and George, 1977; Curry, 1978; Foster and Bates, 1978; Wright, 1978; Heit *et al.*, 1980; Leard *et al.*, 1980; Imlay, 1982; Farrington *et al.*, 1987; Wade *et al.*, 1988a; Lakshmanan and Nabisan, 1989; Naimo *et al.*, 1992). Since the organization of the International Mussel Watch program in 1978, species of the genus *Mytilus* have been used as standard biomonitors in temperate waters of the Pacific and Atlantic coasts (Stephenson *et al.*, 1980; NOAA, 1989). Several species of oysters have been used in warm waters of the southern Atlantic and the Gulf of Mexico (Wade *et al.*, 1988b; NOAA, 1989). However, no suitable species has been identified as a biomonitor of lower rivers and low salinity estuaries, which are often heavily industrialized and populated (NOAA, 1989).

The estuarine clam *Rangia cuneata* (Gray, 1831) fulfills many of the criteria considered necessary for biomonitor species as proposed by Neff *et al.* (1976), the National Research Council (1980), Mason (1991), Havlik and Marking (1987), and Farrington *et al.* (1987). *R. cuneata* is a true estuarine species and occurs naturally where salinity varies between 0-18 ppt (LaSalle and de la Cruz, 1985). It occurs in riverine, bay, and marsh lake estuaries from Campeche, Mexico, to Florida along the Gulf of Mexico and from Florida to Maryland along the Atlantic coast (Gallagher and Wells, 1969; Hopkins and Andrews, 1970; Hopkins *et al.*, 1973). Salinity is limiting only during the planktonic larval stage and adult *R. cuneata* can be transplanted into freshwater or higher salinity water (Hopkins *et al.*, 1973; Cain, 1975). *R. cuneata* has a long life span and shell length can be related to age (Fairbanks, 1963; Wolfe and Petteway, 1968; Gooch, 1971; Hopkins *et al.*, 1973), allowing a reasonable estimate of exposure time. It is a non-selective filter feeder and ingests large quantities of detritus and plankton and is eaten by many consumers that are eaten by humans (Gooch, 1971; Hopkins *et al.*, 1973; LaSalle and de la Cruz, 1985). Another desirable characteristic of *R. cuneata* as a biomonitor is a wide toler-

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ance for many environmental factors, including temperature (Gallagher and Wells, 1969), substratum type (Tenore *et al.*, 1968; Tarver, 1972; Swingle and Bland, 1974), oxygen concentration (Chen and Awapara, 1969; Harrel *et al.*, 1976; Harrel and Hall, 1991), certain heavy metals (Olsen and Harrel, 1973; USEPA, 1984a, b; Eisler, 1988), petroleum-derived aromatic hydrocarbons (Neff *et al.*, 1976), certain insecticides and herbicides (Chaiyarach *et al.*, 1975; Lunsford and Blem, 1982), and polychlorinated dioxins and furans (Harrel and McConnell, 1995).

The purpose of this research was to investigate the use of *Rangia cuneata* as a biomonitor of the heavy metals copper, chromium, cadmium, and lead by determining accumulation rates and concentrations under laboratory and field conditions. Evidence from the literature indicates that the uptake and loss of pollutants, including metals, by bivalves is influenced by the reproductive phase of the test organism (Phillips, 1976; National Research Council, 1980; Simpson, 1979; Van Hattum *et al.*, 1991). Therefore, the reproductive state and percent gonadal biomass were determined throughout this study in order to relate survival of test animals and differences in accumulation of metals to reproductive phase. A detailed account of this study is the subject of another paper, but some of the data will be used to explain the results of this study. Neff *et al.* (1976), Lunsford and Blem (1982), and Harrel and McConnell (1995) have shown that *R. cuneata* is an effective bioaccumulator of certain organic compounds. This study will furnish information needed to determine if *R. cuneata* is an effective accumulator of metals, and could serve as a standard biomonitor species for inland coastal waters and estuaries along the southern Atlantic and the Gulf of Mexico.

MATERIALS AND METHODS

All clams used in this study were collected from Fence Lake, Jefferson County, Texas. This coastal marsh lake is located between the Intracoastal Waterway and the Gulf of Mexico, and has no known history of environmental contamination. Only clams between 40-60 mm (4-6 yrs old) were utilized to minimize size or age differences. The clams were transported in Fence Lake water to the laboratory where the water temperature was allowed to adjust to 16°C to inhibit gametogenesis (Hopkins *et al.*, 1973). They were then transferred to aquaria containing aerated, reconstituted ($NaHCO_3$, $CaSO_4 \cdot H_2O$, $MgSO_4$, KCl) reagent grade II water (Peltier and Weber, 1985) for 48 hrs of acclimation and depuration before being used in laboratory or field exposure experiments.

Laboratory exposures were conducted between April 1991 and August 1992. Between 75-100 clams were placed in glass aquaria in 40 l of reconstituted reagent grade II water and one of the metal salts. Concentrations for chromium and copper were based on an approximate 5% solution of the 96-hr LC_{50} determined by Olsen and Harrel (1973). The Texas Natural Resource Conservation Commission considers this to be a safe concentration of a persistent toxin in receiving waters. Cadmium and lead concentrations were based on the USEPA's (1984a, b) criteria for safe concentration of specific toxic materials for freshwater exposure and calculated as follows: Lead = (1.273[ln hardness]-1.460); cadmium = (1.128[ln hardness]-1.674). The metals were delivered in the following forms and target concentrations; copper (26 µg/l) as copper sulfate, chromium (19 µg/l) as potassium dichromate, cadmium (23 µg/l) as cadmium chloride, and lead (32 µg/l) as lead acetate. Aquaria containing the same number of clams in reconstituted reagent grade II water without any added metals served as controls. Clams and water were collected after 0, 5, 10, 20, and 40 d exposures for analysis of metals. Depuration rates of lead were determined using 60 clams exposed for 40 d to 35 µg/l lead. These clams were placed in 40 l of lead-free water and after 10, 20, and 40 d the clams were collected for lead analysis. Aeration and circulation for all aquaria used in the laboratory study were provided by high volume aerator pumps and diffusion stones.

A lab retention study was performed to test the possibility of sustaining *Rangia cuneata* in captivity over long periods in order to avoid complications associated with reproduction. The clams were collected in January during the spent reproductive phase. From January to September 1992, 40 clams ranging in size from 40-60 mm were maintained in 45 l of reconstituted reagent grade II water (salinity ≤ 0.5 ppt) at 16°C. The clams were fed finely ground Tetra® fish food weekly. In January, March, June, and September, 8-10 clams were excised from the shell, the whole wet tissue was weighed, and the gonadal tissue was dissected from somatic tissue. The tissue was desiccated at 95°C for 24 hrs and then the total tissue biomass, percent gonadal biomass, and percent water were determined.

Accumulation of metals under field conditions was investigated during June-July and October-November 1991 by transplanting laboratory-acclimated clams below two industrial effluent outfalls that contained some of the metals of interest. Both outfalls were located in the Neches River estuary about 5 km upriver from Sabine Lake, a shallow inlet off the Gulf of Mexico. Field exposure Site 1 was located along the margin of the Neches River approximately 100 m below the confluence with Star Lake Canal which receives treated petrochemical effluent. At this site 200 clams were placed directly on the bottom in two 1 m^2 quadrats at a depth of 1 m. Exposure Site 2 was located in an oil refinery effluent canal approximately 200 m below the outfall and 600 m above the confluence with the Neches River. At Site 2, 200 clams were placed in nylon mesh bags and suspended 1 m below the surface (2 m total depth). At both sites, 16-20 clams, water, and sediments were collected after 0, 5, 10, 20, and 40 d exposures for analysis of metals. Both sites were subjected to tidal influences from Sabine Lake and water temperature, salinity, conductivity, pH, and alkalinity concentrations were measured at the end of each exposure period.

Water and sediment samples were collected, preserved, and digested following USEPA Methods 3020 and 3050 (USEPA, 1986; APHA-AWWA-WPCF, 1989). Clam tissue was removed from the shell and frozen until digestion. Digestion was conducted according to USEPA Method 3050 and a modification of Boyer (1984). Metal analyses were performed by atomic absorption spectrophotometry on either a Perkin-Elmer Model 2100 or a Perkin-Elmer Model 5100 spectrophotometer, both with graphite furnace capability, using USEPA Methods 7000 (USEPA, 1986). A quality assurance project plan was implemented prior to beginning sample analysis according to Verner (1990). The data quality indicators precision and bias were estimated with the use of sample blanks (reagent and procedural), as well as spiked and duplicate samples. Data points from the measurements were plotted on quality control charts designed to satisfy a 95% confidence level with an interval of ± 3 standard deviation (Verner, 1990).

Metal concentrations were expressed as µg/l for aqueous samples and µg/kg (wet weight) for tissue and sediments. Bioconcentration factors (BCF), defined as the ratio of the metal concentration in the tissue to the metal concentration in the water, were calculated for all laboratory experiments. The BCF ratio is regarded as a valid indicator of the capacity of a material to accumulate in animal tissue (Davis and Dobbs, 1984). The BCF was calculated using the following equation: $BCF = C_{an} - C_{a0}/C_w$, where C_{an} is the concentration of the metal in the tissue at day n, C_{a0} is the concentration in the tissue at day 0, and C_w is the concentration of the metal in the water.

Relationships between exposure time and metal concentration were determined with the Pearson product-moment correlation coefficient test (Glantz, 1992). Significance of accumulation trends were tested with one-way ANOVA, provided that Bartlett's tests of homogeneity of variance established the data as being parametric (Keystat, 1985). If the data were non-parametric the Kruskall-Wallis test was used. A one-way ANOVA and summary statistics were used to determine if significant weight loss occurred in laboratory-retained clams.

RESULTS

LABORATORY EXPOSURES

During all laboratory exposures the physicochemical conditions were relatively uniform; salinity < 0.5 ppt, water temperature 17° ± 1°C, pH 7.1-7.3, $CaCO_3$ hardness 41-45 mg/l, and alkalinity 30-34 mg/l.

Series 1 copper exposure indicated no accumulation in the tissue at 5 d and marked accumulation between d 5 and d 40 (Table 1). Exposure medium copper concentrations declined approximately 50% by d 5, then remained relatively stable. Bioconcentration factors (BCF) increased from 0 at d 5 to 73 at d 40 with a correlation coefficient (r) between metal concentration and exposure time of 0.82. Background concentrations of copper in the control water ranged from 15-19 µg/l and resulted in accumulation of copper in the control animals, but at a decreased rate and lower final concentration (control mean 1980 µg/kg; exposure mean 3434 µg/kg). Copper water lines were responsible for the excessive copper in the control water.

Series 2 copper exposure resulted in a steady increase in tissue copper concentration over the 40 d period, but at a decreased rate and lower final concentration than in Series 1 (Table 1). A one-way ANOVA of 40 d tissue copper concentration values between Series 1 and 2 indicated no significant difference ($p > 0.05$). BCF values ranged from 9 at d 5 to 26 at d 40 and the correlation between concentration and exposure time was $r = 0.60$. The control group water for Series 2 was also found to contain copper due to exposure to copper water lines (18-23 µg/l) and resulted in an increase in tissue copper concentrations in control animals. However, increases in tissues of the expo-

Table 1. Laboratory exposures of *Rangia cuneata* to copper including exposure water and tissue copper concentrations with corresponding bioconcentration factors (BCF). Tissue means in µg/kg ± standard error of the mean.

EXPOSURE (days)	N	WATER (µg/l)	TISSUE MEAN (µg/kg)	BCF
SERIES 1 (9 April to 19 May 1991)				
0	1	42.2	1735.5	–
5	2	20.6	1700.2 ± 223	0
10	2	30.1	2754.4 ± 54	33.9
20	2	21.7	2764.1 ± 187	47.4
40	1	23.3	3434.3	72.9
Series 2 (10 May to 19 June 1991)				
0	1	40.3	1893.2	–
5	2	50.1	2256.1 ± 447	9.0
10	3	40.5	2518.3 ± 90	15.4
20	2	30.9	2541.4 ± 10	21.0
40	3	30.5	2684.5 ± 44	25.9
Series 3 (16 December 1992 to 5 January 1993)				
0	6	23.2	1745.8 ± 163	–
5	8	23.0	2030.8 ± 60	12.4
10	8	20.9	1995.7 ± 133	10.9
20	8	19.4	2165.0 ± 136	21.6

sure group were again more rapid than in the control group. No mortalities were observed in either series.

Series 3 copper exposure, conducted during December 1992-January 1993, was terminated after 20 d due to mortalities in both the control and exposure groups. The mortalities were believed to be related to a high gonadal biomass burden. Gonadal biomass was 39% of total biomass and could have resulted in the inability to osmoregulate at a salinity ≤ 1 ppt (unpublished data). Series 3 copper exposure resulted in moderate accumulation from an initial mean concentration of 1746 to 2031 µg/kg after 20 d (Table 1). Day 20 mean tissue copper concentration was significantly higher than the initial concentration ($p < 0.05$), but the r value of 0.36 indicated a weak relationship between exposure time and concentration. The BCF values ranged from 12-22 (Table 1). The Series 3 control group water was below detection level (2.0 µg/l), while control tissue means ranged from 1746 µg/kg (d 0) to 1760 µg/kg (d 20). Water used in this series was obtained from a different source to remedy the copper contamination problem.

Series 4 chromium exposure tissue concentration means ranged from 559 µg/kg (d 0) to 2670 µg/kg (d 40) and the correlation between exposure time and concentrations was r = 0.92 (Table 2). BCF values ranged from 33 at d 5 to 422 at 40 d. The control group water concentration ranged from 3-4 µg/l, but control group tissue concentrations ranged from 559 µg/kg (d 0) to 299 µg/kg (d 40) indicating previous exposure to chromium and depuration.

Series 5 chromium exposure resulted in a slow initial, but increasing accumulation trend (Table 2). BCF values ranged from 0.1 (d 5) to 14 (d 40). The marked difference between the tissue concentrations and the BCF values for Series 4 and 5 may be due to initial concentration disparities (Series 4, 559 µg/kg; Series 5, 129 µg/kg).

Table 2. Laboratory exposures of *Rangia cuneata* to chromium including exposure water and tissue chromium concentrations with corresponding bioconcentration factors (BCF). Tissue means in µg/kg ± standard error of the mean.

EXPOSURE (days)	N	WATER (µg/l)	TISSUE MEAN (µg/kg)	BCF
SERIES 4 (9 April to 19 May 1991)				
0	1	11.0	559.1	–
5	2	7.0	787.8 ± 63	32.7
10	2	8.0	1508.7 ± 365	118.7
20	2	9.0	1581.8 ± 171	113.6
40	3	5.0	2670.4 ± 248	422.3
SERIES 5 (10 May to 19 June 1991)				
0	1	11.0	128.6	–
5	3	11.0	129.7 ± 6	0.1
10	3	10.0	143.2 ± 5	1.5
20	3	7.0	154.8 ± 8	3.7
40	2	7.0	226.9 ± 36	14.0

Series 6 lead exposure exhibited the most rapid accumulation of any of the metals tested in the laboratory. Initial tissue concentrations were below detection level (100 µg/kg) and increased by d 40 to 3170 µg/kg (Table 3). BCF values ranged from 25 at d 5 to 93 at d 40. The correlation between exposure time and tissue lead concentration was r = 0.84. The control group lead concentrations were below the detection level in both the water (1.0 µg/l) and *Rangia cuneata* tissues during the entire exposure.

Depuration of lead from Series 6 test animals was conducted by placing clams exposed to lead for 40 d into lead-free water and analyzing the tissues after d 10, 20, and 40. Tissue lead concentration steadily decreased from 3170 µg/kg at d 0 to 984 µg/kg at d 40 (Table 3).

Series 7 exposure to cadmium resulted in a continuous uptake of the metal throughout the 40 d test (Table 4). Analysis of *Rangia cuneata* tissues at initial exposure revealed a concentration of 103 µg/kg with accumulation of cadmium after 40 d exposure to 1151 µg/kg. Cadmium exposure water remained relatively constant with individual measurements ranging from 22-24 µg/l. BCF ratios varied from 8 after 5 d to 44 after 40 d. The correlation coefficient (r) between exposure time and cadmium concentration was 0.75. Control group exposure medium concentration remained below the limit of detection (1.0 µg/l) during the entire 40 d exposure, while tissue levels ranged from 102 µg/kg at initial exposure and declined to 88 µg/kg after 40 d.

LABORATORY RETENTION

Laboratory retention of *Rangia cuneata* from January-September 1992 in 16°C water resulted in inhibition of gonadal tissue hypertrophy, as indicated by relative-

Table 3. Lead laboratory exposure and depuration study of *Rangia cuneata* including exposure water and tissue lead concentrations with corresponding bioconcentration factors (BCF) for lead exposure group. Tissue means in µg/kg ± standard error of the mean.

EXPOSURE (days)	N	WATER (µg/l)	TISSUE MEAN (µg/kg)	BCF
SERIES 6 (15 April to 25 May 1992)				
0	6	38.5	< 100.0	–
5	4	36.1	900.0 ± 162	25.0
10	9	37.7	1863.8 ± 87	49.3
20	7	33.1	2218.3 ± 188	67.0
40	7	33.8	3170.0 ± 331	93.8
DEPURATION STUDY (25 May to 3 July 1992)				
10	7	< 1.0	2243.2 ± 113	–
20	8	< 1.0	1988.4 ± 79	–
40	7	< 1.0	983.9 ± 54	–

Table 4. Laboratory exposure of *Rangia cuneata* to cadmium including exposure water and tissue cadmium concentrations with corresponding bioconcentration factors (BCF). Tissue means in µg/kg ± standard error of the mean.

EXPOSURE (days)	N	WATER (µg/l)	TISSUE MEAN (µg/kg)	BCF
0	5	22.3	102.9 ± 15	–
5	6	25.4	299.5 ± 29	7.8
10	8	21.8	798.9 ± 94	31.9
20	9	23.1	988.9 ± 118	38.4
40	11	23.6	1150.7 ± 88	44.4

ly stable percent gonadal biomass for the duration of the nine month laboratory retention. Percent gonadal biomass in January was 12%, and declined to 11% in March, when Fence Lake clams had a gonadal biomass of about 18%. Laboratory-retained clams percent gonadal biomass increased slightly by June to 14%. In September when Fence Lake *R. cuneata* were ripe and contained over 40% gonadal biomass, the laboratory-retained clams contained only 16% gonadal biomass (Table 5). A significant difference occurred between percent gonadal biomass of laboratory-retained clams and Fence Lake clams ($p < 0.05$). In addition, no significant change was observed in somatic tissue weight between the laboratory and Fence Lake clams ($p < 0.05$), indicating that nutritional deficiency was probably not a factor. However, an essential nutrient required for gonadal development may not be present in the supplement and could have contributed to these findings. Nonetheless, these data suggest that *R. cuneata* can be successfully maintained in the laboratory under controlled conditions over extensive periods of time with no apparent adverse effects. In addition, gametogenesis can be successfully inhibited, thus avoiding complications associated with changing reproductive status.

FIELD EXPOSURES

Physicochemical conditions varied considerably between the two field exposure sites (Table 6). Most of these differences were due to freshwater conditions in the river during the exposure at Site 1 and the occurrence of salt water intrusion during the exposure at Site 2.

At Site 1 mean copper concentrations in *Rangia cuneata* tissues increased from 2240 µg/kg (d 0) to 2734 µg/kg (d 40) (Fig. 1). The initial and the 40 d tissue concentrations were significantly different ($p < 0.05$), but there was a weak relationship between exposure time and tissue copper concentration ($r = 0.46$). Water samples collected at this site had copper levels below the level of detection (0.01 µg/l). Copper concentrations in the sediments ranged from 3791-5647 µg/kg, indicating prior contamination. Copper accumulation by *R. cuneata* at Site 2 followed a similar trend compared to Site 1, but with slightly less uptake (Fig. 2). Tissue copper concentration means for the initial and 40 d periods were significantly different ($p < 0.05$). Sediment concentrations were highly variable (1641-4045

Table 5. Seasonal changes in biomass (dry weight) as related to temperature and salinity for Fence Lake and laboratory retained *Rangia cuneata.*

TIME	N	MEAN GONADAL BIOMASS (%)	MEAN WT. (g)	TEMPERATURE (°C)	SALINITY (ppt)
Sept. 1991	5	49	1.33	30	2.7
Oct.	5	24	0.70	20	3.0
Nov.	7	18	0.61	16	5.0
Dec.	10	15	0.43	16	3.8
Jan. 1992	8	12	0.60	16	1.5
Feb.	10	18	0.66	16	1.0
Mar.	10	18	0.68	19	1.5
June	9	23	0.76	23	5.5
July	10	38	1.15	28	9.5
Sept.	12	40	1.21	30	10.5
Oct.	10	27	0.85	23	12.0
Dec.	20	39	0.95	15	7.0
Laboratory Retention Study					
Jan. 1992	8	12	0.60	16	1.5
Mar.	8	11	0.57	17	< 1.0
June	9	14	0.63	16	< 1.0
Sept.	10	16	0.66	16	< 1.0

Table 6. Physicochemical conditions for the field exposure Sites 1 (June-July) and 2 (September-November).

	TEMPERATURE (°C)	pH	SALINITY (ppt)	ALKALINITY (mg/l)
Site 1	28-34	7.1-7.6	< 0.5	29-36
Site 2	20-25	8.4-8.9	5-9	50-73

μg/kg), probably due to heterogeneous sediment composition.

The pattern of chromium uptake by *Rangia cuneata* was similar at Sites 1 and 2 (Figs. 3 and 4). The 40 d tissue concentration at Site 1 was 99 μg/kg, and at Site 2, 242 μg/kg. Significant differences were demonstrated between the initial and 40 d concentrations at both sites ($p < 0.001$), however no correlation existed between exposure times and concentrations (Site 1, $r = 0.18$; Site 2, $r = 0.21$). Chromium concentrations in the water ranged from 0.07-0.52 μg/l at Site 1 and 2-3 μg/l at Site 2. At both sites the concentration of chromium in the sediment was high and variable, again probably due to differences in sediment type.

Cadmium tissue concentrations were variable at both sites (Figs. 5 and 6). Comparison of initial and 40 d tissue concentrations indicated significant difference ($p < 0.05$) at Site 1, but not at Site 2. The correlation coefficients between exposure time and tissue cadmium concentrations were 0.36 (Site 1) and 0.13 (Site 2). At Site 1, cadmium concentrations in the water ranged from 0.06-0.22 μg/l and varied from 120-560 μg/kg in the sediments. At Site 2, cadmium water concentrations ranged from 0.17-0.49 μg/l and sediment concentrations ranged from 31-138 μg/kg.

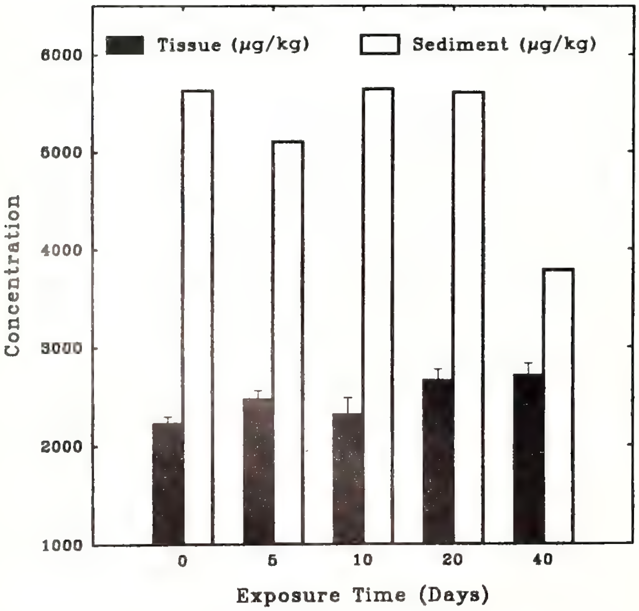

Fig. 1. Uptake of copper by *Rangia cuneata* at field exposure Site 1 located below Star Lake Canal in the Neches River.

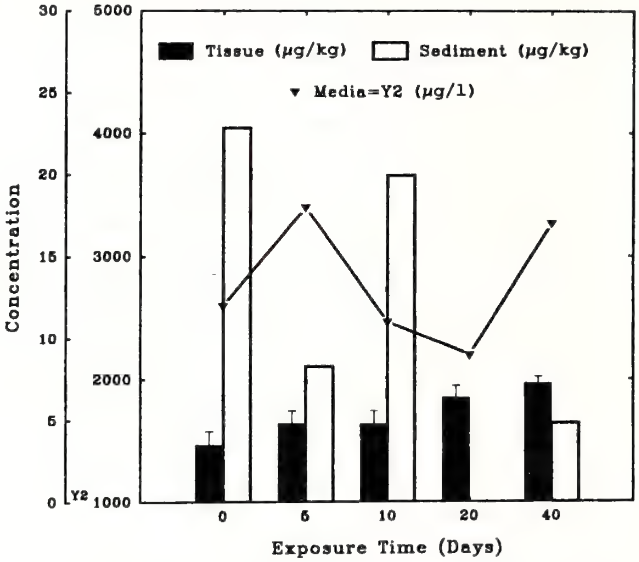

Fig. 2. Uptake of copper by *Rangia cuneata* at field exposure Site 2 located in an oil refinery effluent canal approximately 200 m below the outfall and 600 m above the confluence with the Neches River. Day 20 sediment sample could not be obtained.

Lead concentrations in *Rangia cuneata* tissues varied at both sites (Figs. 7 and 8). An analysis of tissue concentrations at Site 1 indicated no significant change in lead body burden during the exposure ($p > 0.05$). At Site 2 a significant change in tissue lead concentration occurred between the initial and 40 d periods ($p < 0.001$), but the correlation coefficient between exposure time and lead concentrations indicated no relationship ($r = 0.18$). Water lead concentrations at Site 1 ranged from < 0.01-1 μg/l and sediment concentrations were 9890-15429 μg/kg.

DISCUSSION AND CONCLUSION

By performing laboratory exposures to metals many environmental variables were eliminated and metal speciation was predictable (Pankow, 1991). Field exposures tested the organism's performance as a biomonitor in complex and highly labile environments. Even though the test animals were collected from an isolated lake with no known history of contamination, analysis of tissue metal concentrations at exposure d 0 showed that a significant body burden of all of the metals, except lead, occurred.

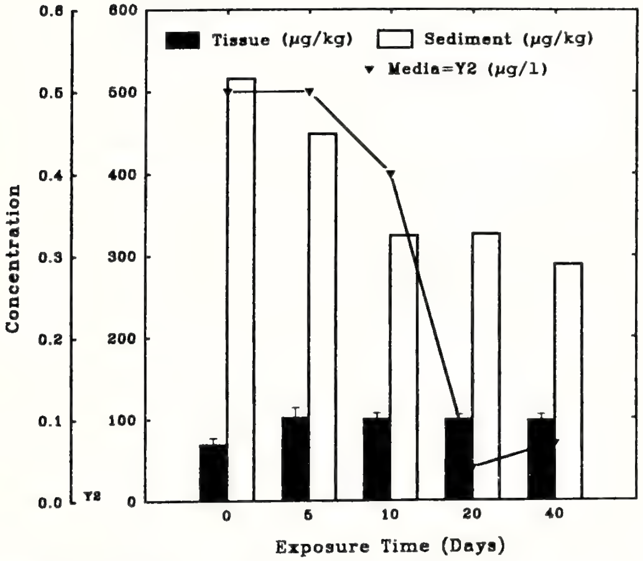

Fig. 3. Uptake of chromium by *Rangia cuneata* at field exposure Site 1 located below Star Lake Canal in the Neches River.

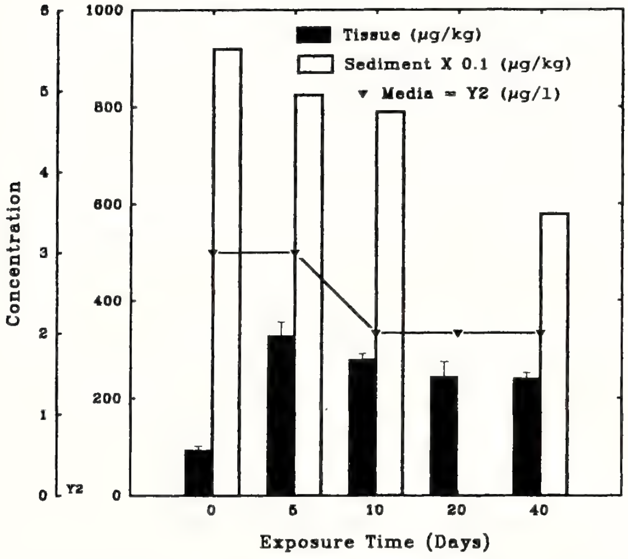

Fig. 4. Uptake of chromium by *Rangia cuneata* at field exposure Site 2 located in an oil refinery effluent canal approximately 200 m below the outfall and 600 m above the confluence with the Neches River. Day 20 sediment sample could not be obtained.

Laboratory and field exposures to copper demonstrated uniform metal uptake (Table 1, Figs. 1 and 2). Little difference was found in the uptake rate of copper from all exposures even though different seasonal periods were represented. However, the laboratory Series 3 copper exposure, conducted during December and January had to be terminated due to mortalities in both the exposure group and the control group. These mortalities occurred when the clams had a gonadal biomass equivalent to 39% of their total body biomass, possibly interfering with osmoregulatory processes. This hypothesis is consistent with later observations which evaluated seasonal trends in *Rangia cuneata* osmoregulation capacity in salinities ranging from < 0.50-20 ppt (unpublished data). Conditions in the laboratory favored the ionic Cu^{+2} form which is usually the most bioavailable and toxic form of copper (Pankow, 1991; Giesy *et al.*, 1983). The species of copper *R. cuneata* was exposed to in the field is unknown. However, the cupric ion is highly reactive and forms complexes and precipitates with many inorganic and organic constituents of natural waters (USEPA, 1980). Thus, the proportion of ionic copper in the field was probably low. This suggests that several mechanisms of copper uptake occurred, because both laboratory and field exposures contained similar results. Bray *et al.* (1983) reported an inducible metal binding protein similar to metallothioneins in *R. cuneata*, while Roesijadi (1980) found increased tolerance to copper associated with synthesis of metallothioneins. Thus, long term exposure to copper in Fence Lake could have induced the synthesis of metallothionein-like proteins resulting in increased copper tolerance and high copper concentrations in Fence Lake *R. cuneata*. However, even with an already high body burden of copper, *R. cuneata* consistently accumulated copper regardless of exposure time and season.

Accumulation of chromium during the 40 d laboratory exposures was 4.7X and 1.8X the initial tissue concentrations for Series 4 and 5, respectively (Table 2). There was a significant difference in the chromium uptake rates and the final concentrations between the two series ($p < 0.05$) under comparable physicochemical conditions and reproductive phases of the test animals. The Series 4 clams had 4.3X higher initial chromium concentration than Series 5 clams due to prior exposure, which may account for the disparity in uptake results. In the field exposures chromium was not consistently taken up at either site however, Site 2 chromium was significantly higher than at Site 1 ($p < 0.05$) after 40 d of exposure (Figs. 3 and 4). The cause of this inconsistency is not known, but may be related to body weight variations associated with seasonal reproductive state as reported by Phillips (1976). The difference may also be related to the higher concentration of chromium in the sediments and water found at Site 2 and/or physicochemical conditions which favored the species of chromium with greater potential for uptake. Chromium in natural waters can exist in a number of oxidation states with different activities ranging from -2 to +6, but is most often found in the trivalent (+3) and hexavalent (+6) forms (USEPA, 1985). Rapid evolution of chromium in the sediment can occur. Precipitated Cr^{+3} hydroxides in the sediment may solubilize and remain as Cr^{+3} or can be oxidized to Cr^{+6} by

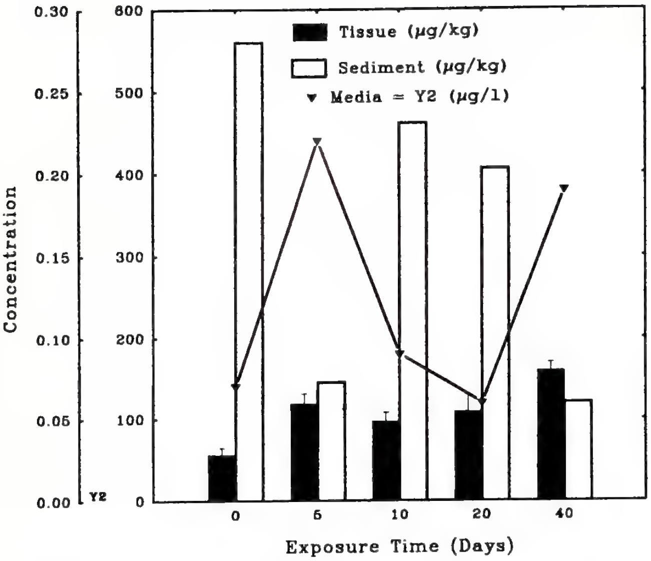

Fig. 5. Uptake of cadmium by *Rangia cuneata* at field exposure Site 1 located below the Star Lake Canal in the Neches River.

aeration. This dynamic transformation was probably a continual process at Sites 1 and 2 where tidal influence, currents, high rainfall and terrestrial runoff, and boat traffic constantly altered sediment redox. In laboratory chromium exposures, the +6 oxidation state was probably favored due to oxygenated conditions and low organic matter, although the trivalent form was likely present as well.

Laboratory exposure to cadmium resulted in rapid accumulation and consistent uptake, with a 11X increase in tissue concentration from d 0 to d 40 (Table 3). Field exposure results did not resemble the laboratory exposure results. At field exposure Site 1, *Rangia cuneata* accumulated cadmium, but uptake was variable during the intermediate exposure period (Fig. 5). At Site 2, no significant uptake of cadmium occurred even though cadmium concentration in the water was usually higher (Fig. 6). These variations were probably due to the disparate physicochemical conditions that existed between the laboratory exposure and the two field exposures. In the laboratory the predominately dissolved species of cadmium was probably free cadmium (Cd^{+2}) which is usually the most toxic and bioavailable form (Winner, 1984; Stackhouse and Benson, 1989). Conditions in the laboratory and at field exposure Site 1 may have favored a larger fraction of cadmium in the Cd^{+2} form as salinity, pH, alkalinity, and water hardness were comparable. Another factor is the role of dissolved organic matter (DOM), which is known to readily alter cadmium toxicity and bioaccumulation properties by changing the concentration of Cd^{+2} in solution through adsorption and desorption processes (Winner, 1984; Eisler, 1985; Stackhouse and Benson, 1989). The DOM concentration at Site 2 may have been higher due to its location (adjacent to marshland), thus rendering less cadmium in the bioavailable form. Also, pH, salinity, alkalinity, and temperature were vastly different between the field exposures and are all known to influence the biological uptake of cadmium (Phillips, 1976; Hung, 1982; Eisler, 1985; Van Hattum *et al.*, 1988).

As with copper, cadmium uptake by *Rangia cuneata* may have been influenced by metal binding proteins. Bray *et al.* (1983) suggested that a structural difference existed between metallothionein species for cadmium and copper, with the possible implication of metal specific induction mechanisms. Induction of a metallothionein-like protein in the benthic oligochaete *Limnodrilus hoffmeisteri* (Laparéde, 1862) was reported to have contributed to cadmium resistance at a metal-polluted site by Klerks and Bartholomew (1991). The resistance was not achieved by a reduction in cadmium but by elevated protein levels and metal sequestering in sulphur rich granules.

In the laboratory, accumulation of lead by *Rangia cuneata* was rapid and highly consistent (Table 4). The BCF values increased from 25 after 5 d to 94 after 40 d. However, in the field exposures lead uptake was slight and erratic despite lead contamination of the sediments (Figs. 7 and 8). The major proportion of lead in the laboratory exposure was probably in the ionic Pb^{+2} form, as revealed from physicochemical data and pH predominance diagrams from Pankow (1991). Wong *et al.* (1978) reported

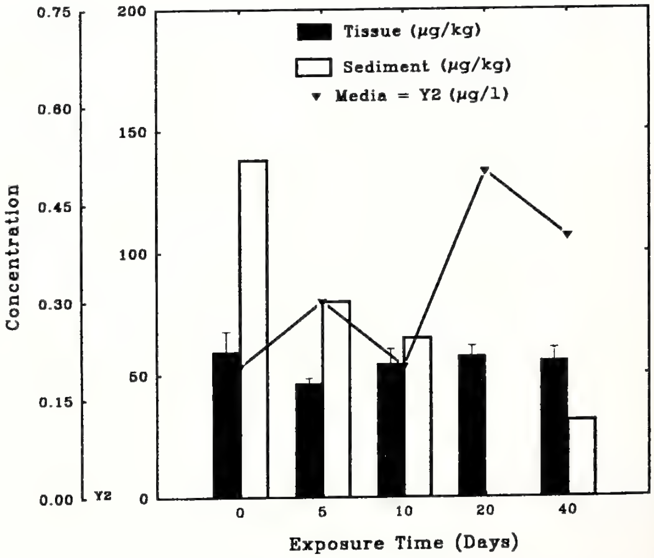

Fig. 6. Uptake of cadmium by *Rangia cuneata* at field exposure Site 2 located in an oil refinery effluent canal approximately 200 m below the outfall and 600 m above the confluence with the Neches River. Day 20 sediment sample could not be obtained.

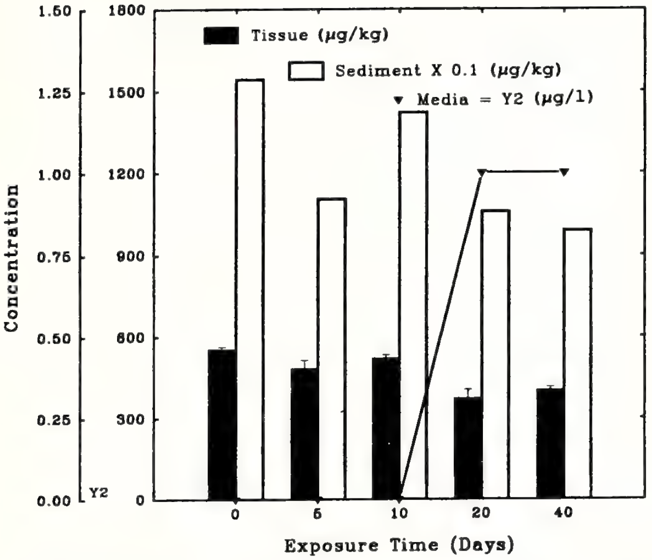

Fig. 7. Uptake of lead by *Rangia cuneata* at field exposure Site 1 located below the Star Lake Canal in the Neches River. Days 0-10 media values were below the limit of detection (0.01 µg/l).

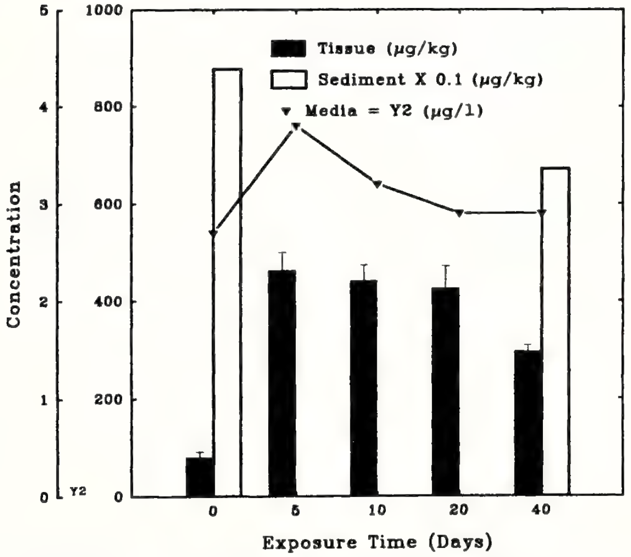

Fig. 8. Uptake of lead by *Rangia cuneata* at field exposure Site 2 located in an oil refinery effluent canal approximately 200 m below the outfall and 600 m above the confluence with the Neches River. Days 5-20 sediment values could not be obtained.

that only soluble waterborne lead is toxic to aquatic biota, and for most cases the ionic forms are more toxic and bioavailable than complexed forms. Lead usually exists in surface waters in three forms: (1) dissolved labile - Pb^{+2}, $PbOH^+$, $PbCO_3$, (2) dissolved bound - colloids or complexes, and (3) particulate (Benes *et al.*, 1985). The predominate species of lead occurs in the dissolved bound form or particulate form when surface waters contain substantial concentrations of DOM (Eisler, 1988). Precipitated lead in the sediment is often tightly bound and characterized by slow release time (Prause *et al.*, 1985). This may explain the low water and high sediment lead concentrations during the field exposures.

A lead depuration study was conducted following Series 6 laboratory exposure. After 10 d, a 29% reduction in tissue lead level was observed. This decrease may have been due to non-bound lead removal from the gills. Production of mucus, primarily in the gills, is a common toxicological response in bivalves and could have influenced removal of trapped lead once transferred to clean water. After 20 d of depuration 63% of the lead remained, indicating a more tightly bound proportion of lead. The half-life of lead in *Rangia cuneata* tissues occurred between the 20 and 40 d depuration periods. Thus, *R. cuneata* is capable of reflecting changing concentrations of lead in the water over time, indicating that metabolic processes do not interfere in the evaluation of lead bioavailability.

Recommendations have been offered to minimize variations in bioaccumulation associated with the reproductive cycle in bivalves (Phillips, 1976; National Research Council, 1980). Phillips (1976) suggested collecting specimens in the same season so as to avoid seasonal changes in body weight. This, however is impractical and places temporal limitations on monitoring strategies. By collecting *Rangia cuneata* during the spent phase and retaining them in a thermally controlled (15-17°C) environment, gametogenesis was inhibited and the gonadal biomass maintained at < 20% of total biomass. Laboratory retained clams were fed regularly and showed no significant decreases in weight. While the possibility remains that an essential nutrient required for gametogenesis was not present in the food supplement, at present, the most rational explanation is that of controlled temperature. It has long been known that temperature is the primary factor regulating gametogenesis in *R. cuneata* (*fide* Hopkins *et al.*, 1973). Thus, by understanding the mechanisms which regulate reproduction, strategies can be implemented to circumvent seasonal complications associated with the use of *R. cuneata* as a biomonitor.

Laboratory and field exposures seemed to indicate that *Rangia cuneata* is a suitable biomonitor of the most biologically active forms of copper, chromium, cadmium and lead. In addition, its extreme tolerance to varying environmental conditions, wide geographical distribution, occurrence in high densities, and knowledge of factors that regulate its life cycle all support the use of *R. cuneata* as a biomonitor of hazardous substances. *R. cuneata* can be conveniently transplanted into inland waters or estuaries, thus extending the Mussel Watch effort to sensitive areas along our coastlines which previously have been neglected

(NOAA, 1989). However, more work is required to evaluate the many factors that control metal uptake during bioaccumulation trials.

ACKNOWLEDGMENTS

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Ecological notes and patterns of dispersal in the recently introduced mussel, *Perna perna* (Linné, 1758), in the Gulf of Mexico

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Abstract. Invasive mussels, *Perna perna* (Linné, 1758), were first detected in south Texas on the jetties at Port Aransas (27° 50' N) in February 1990 (Hicks and Tunnell, 1993). Within four years the species has colonized jetties, navigation buoys, petroleum platforms, wrecks, and other artificial hard substrata as well as natural rocky shores between Matagorda Peninsula (28° 35' N), Texas, and Playa Escondida (18° 35' N), southern Veracruz, Mexico, a distance of over 1,300 km. Densities of 27,200/m^2 small individuals (mean = 16 mm ± 0.3 SE) have been recorded from south Texas jetties. Spat settlement densities of up to 300/25 cm^2 (120,000/m^2) have been recorded from algal substrata in southern Veracruz, Mexico. On oil production platforms, 6-27 km offshore from Port Aransas, the species occurs from the intertidal zone down to depths of 9 m. Dispersal patterns interpreted from discovery data in the Gulf of Mexico indicate a primarily southward expansion from the initial recording. The occurrence of *P. perna* in euryhaline environments, such as river mouths and bay systems, demonstrates the ecological adaptability of this species.

Perna perna (Linné, 1758) (Mytilidae) was first detected in south Texas on the jetties at Port Aransas (27° 50' N) in February 1990 (Hicks and Tunnell, 1993). Within four years jetties, navigation buoys, petroleum platforms, wrecks, and other artificial hard substrata as well as natural rocky shores between Matagorda Peninsula (28° 35' N), Texas, and Playa Escondida (18° 35' N), southern Veracruz, Mexico, a distance of over 1,300 km, had been colonized. Although the species was first detected at Port Aransas, the establishment of high-density beds there and to the north has been relatively slow compared to recently colonized areas to the south. Worldwide records of geographic distribution for *P. perna* include: Aden, the Red Sea, Madagascar, the east coast of Africa from central Mozambique to False Bay in the Cape, the African west coast from Luderiz Bay northwards, the Mediterranean from Gibraltar to the Gulf of Tunis, Brazil, Uruguay, Venezuela, the West Indies, and the Straits of Magellan (Berry, 1978). This paper documents the current status of this recently introduced species and demonstrates its dispersal through an examination of the chronology of discovery and settlement patterns from locations along the western Gulf of Mexico coastline.

Perna perna is opportunistically colonizing hard substrata in the southwestern Gulf of Mexico, settling on jetties and debris (natural and artificial) in the surf zone as well as on offshore oil production platforms and navigation buoys. Locally (Port Aransas to Brazos Santiago Passes), individuals dominate the lower mid-intertidal zone of granite jetties, forming a distinct "mussel belt" (Fig. 1). Densities of up to 27,200/m^2 small individuals (mean = 16 mm ± 0.3 SE) have been recorded from jetty rock. Jetties commonly support densities of 10,000-12,000/m^2. The species has also been found colonizing the skeletal structures of petroleum platforms and navigation buoys along the south Texas coast as far as 27 km offshore from Port Aransas, Texas. On petroleum platforms, *P. perna* colonizes structures from the intertidal zone down to depths of 9 m. This aggressive new member of the fouling community in the Gulf of Mexico has the potential to dramatically increase the maintenance and or replacement interval of offshore navigation aids. The concern is that heavy infestations could partially sink navigation buoys and affect shipping safety. In Brazil, a native locality, the navy is responsible for maintaining navigation buoys, and has to remove fouling layers due to *P. perna* infestations every six months (E. C. Rios, pers. comm., 1994). The U.S. Coast Guard's "Aids to Navigation Team" is currently responsible for maintaining approximately 150 navigation buoys in the nearshore waters of the Gulf of Mexico annually.

Mytilids are known to be responsible for the formation of complex biological substrata (Paine, 1976). Mussels attach to the substratum and to one another by a dense network of byssal threads, forming a trap for particulate debris. The mussel matrix and trapped material encrust the underlying substratum, preventing the attachment of other sessile organisms, including their own recruits. On artificial substrata in south Texas, beds can be composed of

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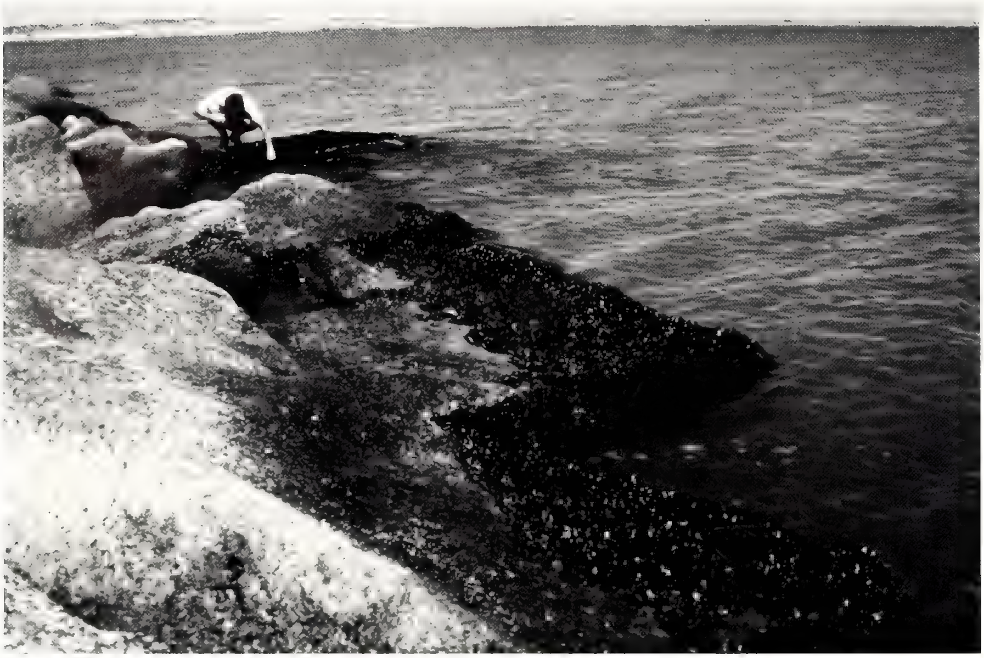

Fig. 1. Mussel belt on the north side of the north Port Mansfield jetty in August 1994.

several layers and attain thicknesses in excess of 20 cm. Mussels taken from the interior of clumps are often deformed and twisted as reported by Harger (1972) for two species of *Mytilus* in California. This modification of the primary substratum results in both the displacement and facilitation of other sedentary species. Sessile organisms dominating this zone prior to the *Perna* introduction include cirripedes, *Balanus* spp. and *Chthamalus fragilis* Darwin, 1854; red algae, *Hypnea musciformis* (Wulfen) Lamouroux, 1813, and *Centroceros clavulatum* (C. Agardh) Montagne, 1846; anemones, *Bunodosoma cavernata* (Bosc, 1802); and other mussels, *Brachidontes exustus* (Linné, 1758).

Lower mid-intertidal hard substrata available for *Perna perna* colonization in south Texas are primarily groins and jetties, and have existed for only a century (Britton and Morton, 1989). Therefore, the invasion by *P. perna* in south Texas is not disrupting a co-evolved, natural assemblage. However, to the south, the species is rapidly invading the unique volcanic outcroppings of central Mexico that occur from approximately 24° N latitude to the Tuxtlas Mountain Province southeast of the city of Veracruz. The presence of mussel beds will inevitably bring about physical modifications to the natural substratum and therefore impact these natural communities. Dominant sessile molluscan species in the lower intertidal zone of this natural rocky shore area, prior to the introduction, were *Petaloconchus varians* (Orbigny, 1841), *Brachidontes exustus* (Linné, 1758), and *Isognomon bicolor* (C. B. Adams, 1845) (Wiley *et al.*, 1982).

METHODS

Discovery data for *Perna perna* in the Gulf of Mexico were organized from various sources including literature, personal communications, University collections, and field trips. Data were then used to interpret dispersal patterns since the initial discovery. Density and length-frequency data, when available, were determined from collected mussel clumps where clump size and individual lengths were measured to the nearest centimeter and millimeter, respectively.

RESULTS

The dates of first discovery of *Perna perna* at locations in the Gulf of Mexico are given in Fig. 2. The localities depicted represent only those sites for which a history of collection data were available and do not represent the only sites from which the species is known. Thorough collecting efforts on the south jetty at Port Aransas (27° 50' N) in February 1990 yielded only two specimens, each 20 mm in length. Growth data for *P. perna* from Durban, South Africa (29° 52' S) (Berry, 1978), as well as from the Gulf of Mexico (unpublished) indicate that these first specimens had settled approximately two months earlier. First discovery of individuals on the north jetty at Port Mansfield (26° 33' N), approximately 230 km south of Port Aransas, occurred in September 1991. At that time, individuals were widely spaced (≤ 200 individuals/m^2), did not form extensive beds, and appeared to be of the same size class. Three specimens representing the range in length were collected (50, 51, and 55 mm). In July 1992, the species was first discovered at the Brazos Santiago Pass jetties (26° 04' N) (M. K. Wicksten, pers. comm., 1992). At that time, bed formation was observed on both sides of the north jetty. Three representative specimens were collected (12, 32, and 32 mm; M. K. Wicksten, pers. comm. 1992). No mussels were found at the Brazos Santiago Pass jetties during a previous visit in March 1990.

From the jetties at La Pesca, Mexico (23° 47' N), in March 1990, and the natural rocky shores at Boca Andrea (19° 44' N) and Playa Escondida (18° 35' N), Mexico, in October 1990, no mussels were collected. However, the species was found at these same localities during visits exactly three years later. Extensive mussel bed formation was observed on the jetties at La Pesca, Mexico, in March 1993. Individuals at La Pesca ranged in size from 2-71 mm containing two distinct size classes (means = 9.8 mm ± 0.33 SE and 57.3 ± 0.67 SE). In October 1993, the species was first discovered on the natural rocky shores at Punta Boca Andrea. At that time, bed formation was observed and densities as high as 5,216 individuals/m^2 (mean = 26 mm ± 0.58 SE) were recorded. Sizes of mussels at Boca Andrea ranged from 5-71 mm, representing at least two size classes. The first discovery of *Perna perna* at Playa Escondida also occurred in October 1993; here they were widely spaced and did not form beds. Twenty-five specimens were collected ranging from 18-46 mm (mean = 37 mm ± 1.5 SE). In March 1994, densities of small individuals (2-10 mm) as high as 300/25 cm^2 (120,000/m^2) were observed on algal substratum [*Laurencia papillosa* (C. Agardh) Greville] at the Playa Escondida site. Similar recruitment events were observed in Texas prior to the formation of well-established beds. The individuals collected at Playa Escondida represent the southern end of the species' known distribution in the Gulf of Mexico; however, localities further to the south and east have not been visited.

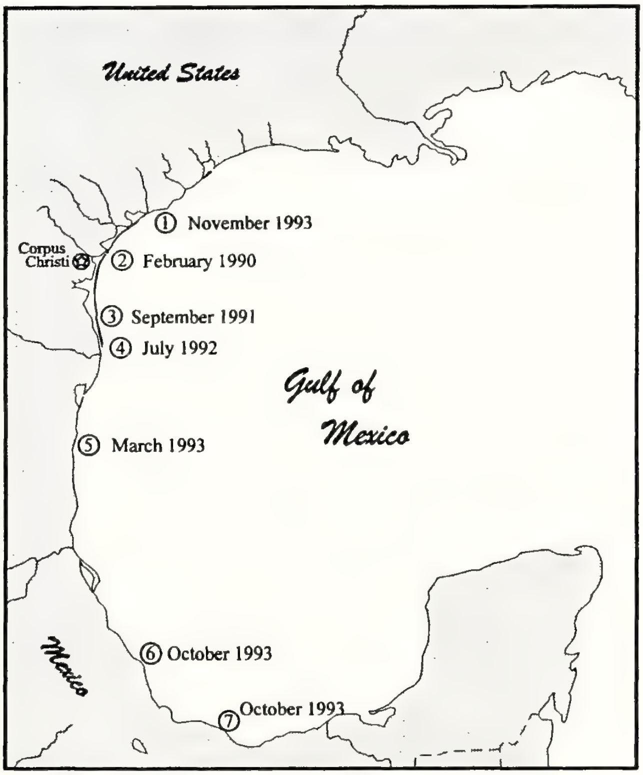

Fig. 2. Locations and dates of first discovery of brown mussels, *Perna perna*, in the Gulf of Mexico: (1) Colorado River; (2) Port Aransas Pass; (3) Port Mansfield Pass; (4) Brazos Santiago Pass; (5) La Pesca; (6) Boca Andrea; (7) Playa Escondida.

To the north, *Perna perna* was collected from the jetties adjacent to the Colorado River on Matagorda Peninsula (28° 35' N), Texas (Davenport, 1994), and from the jetties adjacent to the Gulf Intracoastal Waterway at Port O'Conner (28° 26' N) (Davenport, 1995). A single specimen, 52 mm in length, was collected in November 1993 from the east side of the easternmost jetty on Matagorda Peninsula. During a study of marine macroalgae conducted at the same jetty in 1993, Boyd and Wardle (1994) reported a consistent gulfside salinity of 25 ppt for three months sampled (January-March). Two specimens, each 20 mm in length, were collected in February 1995 from the northernmost jetty at Port O'Conner. The discovery of *P. perna* at Port O'Conner was the first record of the species inhabiting any Texas bay system.

DISCUSSION

The chronology of collection events depict a southward expansion of *Perna perna* from the initial point of discovery, Port Aransas, Texas. Colonization success in areas south of the initial point of discovery is likely the result of hydrographic factors, such as longshore and nearshore-surface currents. Accordingly, the slow establishment of mussel populations to the north is likely due to a lack of incoming recruits, rather than environmental constraints posed by decreasing temperature and salinity gradients from south to north that exist along the Texas coast. Longshore currents flow southeasterly along the upper Texas coast and northeasterly along the southern Texas and northern Mexico coasts, converging at approximately 27° N latitude (Britton and Morton, 1989). The persistent southeasterly direction of longshore and nearshore-surface currents to the north of 27° N is probably responsible for the slow establishment of mussel beds here. Cold fronts, while having only moderate effects on longshore systems to the north have dramatic effects on longshore and nearshore current systems southward along the coastal bend (Watson and Behrens, 1970; Britton and Morton, 1989). The rapid expansion of *P. perna* to the south is likely due to the coincidence of mass spawning events with seasonal changes in current direction. Temperature is one of the more important factors controlling gametogenesis in temperate and subtropical bivalve mollusks (Giese, 1959). Peak spawning periods of *P. perna* have been found to coincide with the season of lowest temperature in South Africa, Angola, Venezuela, and Brazil (Berry, 1978). Spawning peaks of *P. perna* populations in Venezuela and Brazil occur when temperature declines to 22° C after a maximum of 28° C (Lunetta, 1969; Velez and Epifanio, 1981). Conversely, elevated temperature is routinely used in conditioning bivalves to spawn out of season (Loosanoff and Davis, 1963; Velez and Epifanio, 1981). The largest recruitment events in the Gulf of Mexico have been observed during fall and early spring. Major recruitment events were observed at La Pesca in March 1993, Port Mansfield in December 1993 and 1994, and at Boca Andrea and Playa Escondida in March 1994. However, no major recruitment was observed at the Port Aransas or Fish Pass jetties (29 km south of Port Aransas) during these same periods. Only minor recruitments (< 64 individuals/m^2) were observed at these localities during December 1993 and 1994, and May 1994. It is believed that recruitment in areas to the north of approximately 27° N is largely dependent upon deviations from seasonal patterns in current direction and spawning cycles. However, the placement and hard-substratum-type habitat, provided by oil production platforms, could facilitate spread to the north.

The discovery of specimens at the mouth of the Colorado River (157 km north of Port Aransas) and the jetty at Port O'Conner demonstrates the ecological adaptability of *Perna perna*. The length of the individual collected from the Colorado River (52 mm) indicates that it had resided at that location for 7-12 mo (Berry, 1978, and unpublished growth data from the Gulf of Mexico) and is thus tolerant of those conditions (salinity and temperature) characteristic of the northern Texas coast. According to literature (Vakily, 1989), *P. perna* tolerates fairly large fluctuations in salinity, adapting well to ranges of 19-44 ppt. The type locality of the species, the Straits of Magellan (Siddall, 1980), demonstrates its ability to tolerate lower temperatures.

We expect the dispersal of *Perna perna* to the north of Port Aransas to continue, driven by deviations from seasonal patterns in current direction and spawning cycles, and increasing sources of recruitment, as offshore oil production platforms become colonized, but at a much slower rate than has been observed to the south.

ACKNOWLEDGMENTS

We thank B. Hardegree for assistance in the field; N. Sohn, R. Smith, N. Barrera, and S. Alvarado for assistance in the laboratory; and M. K. Wicksten and N. Clements for relating findings of mussels. The manuscript benefited from review by two anonymous reviewers. Current and continuing research is being funded in part by a grant from the Texas A & M Sea Grant College Program.

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AMERICAN MALACOLOGICAL UNION
FINANCIAL REPORT

General Accounts

1994 Income and Expenses

BEGINNING BALANCE (12/31/93)		$96,570.12
INCOME		$27,852.16
Membership Dues	15,658.99	
Interest	2,682.28	
General Bank Account	1,238.11	
Symposium Endowment Fund Accounts	1,444.17	
Publications Income	7,110.17	
AMB Subscriptions	2,853.00	
AMB Back Issues	674.00	
AMB Page Charges	1,898.00	
AMB Reprint Charges	1,656.12	
Sales of Other Publications	29.05	
1993 Annual Meeting	2,653.85	
Net profit	58.62	
Auction (to Symposium Endowment Fund)	1,808.10	
Donation, Student Award	250.00	
Donation, Symposium Endowment Fund	272.00	
Miscellaneous Income	12.00	
EXPENSES		$22,596.34
Office expenses	569.76	
Mailing Costs	3,147.20	
Postage - *AMB*	1,729.42	
Postage - Reprints	273.34	
Postage - AMU Newsletter	675.24	
Postage - Miscellaneous	283.05	
Envelopes	186.15	
Affiliate Memberships	230.00	
Banking Fees	384.25	
Incorporation Fee	5.00	
Insurance/Bond Fees	791.00	
Accounting Fees	265.00	
Publication Costs	13,326.39	
AMB	10,560.00	
Reprints	1,324.76	
AMU Newsletter	1,441.63	
Travel Expenses (officers to meeting)	1,333.67	
Annual Meeting	2,544.07	
Promotions	559.07	
Symposium Expenses	1,100.00	
Student Paper Awards	750.00	
Miscellaneous Expenses	135.00	
NET GAIN IN 1994		$5,255.82
ENDING BALANCE		$99,961.35

AMERICAN
MALACOLOGICAL
UNION
THE FIELD MUSEUM - CHICAGO - 1996

62nd ANNUAL MEETING
THE AMERICAN MALACOLOGICAL UNION
CHICAGO, ILLINOIS
JUNE 29 - JULY 3, 1996

The American Malacological Union will hold its 1996 meeting in Chicago, June 29 through July 3. Site of the meeting will be The Field Museum, one of the world's largest natural history museums, located on the shore of Lake Michigan facing Chicago's spectacular skyline. Several special symposia and workshops are in preparation:

- Shell Power - Molluscan shells as sources of phylogenetic, ecological and anatomical information. Organizer: Geraat J. Vermeij (University of California, Davis). Invited papers.
- Freshwater Mollusks [areas of concentration: (a) Life history/growth and development, (b) Conservation/introduced species, (c) Phylogeny/zoogeography]. Organizers: Arthur E. Bogan (Freshwater Molluscan Research), Kevin S. Cummings (Illinois Natural History Survey), and G. Thomas Watters (Ohio State University). Contributed papers. Contact AEB at bogan@say.acnatsci.org.
- Mollusca and the Internet. Organizer: David R. Lindberg (University of California, Berkeley; drlucmp@cmsa.berkeley.edu).
- Collection Management (chemical and physical processes affecting the preparation and storage of molluscan collections, and the management of collection data). Organizers: Paul H. Scott (Santa Barbara Museum of Natural History), and John D. Slapcinsky (Field Museum). Invited and contributed papers; contact JDS at slapcin@fmnh.org.

In addition, there will be general sessions for contributed papers that are not part of the above. Poster presentations are strongly encouraged. Several awards for student papers and posters will be given.

Housing will be available in the Blackstone Hotel, a historic Chicago hotel located on Michigan Avenue, very close to Chicago's downtown museums, main shopping district, and numerous tourist attractions. Free dormitory housing will be available for students who present papers or posters!

Field trips, special exhibits, evening programs, and a banquet in Field Museum's Stanley Field Hall will be part of the meeting.

The dates (Saturday, June 29, to Wednesday, July 3) have been selected to coincide with tourist activities in Chicago (a food festival and city fireworks). The included Saturday night allows for reduced-rate airfares with most carriers. Chicago's O'Hare Airport (the busiest airport in the world) and the smaller Midway Airport (also with easy access to downtown, and home to several discount carriers), as well as numerous bus and train connections make it easy and relatively inexpensive to get to the meeting. We hope to see you at AMU Chicago '96!

For further information please contact:
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Fax (312) 663-5397

IN MEMORIAM

Harold W. Harry
Walter E. Sage III
Kay C. Vaught

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Dates of Publication
Volume 11(1), December, 1994
Volume 11(2), August, 1995

CONTRIBUTOR INFORMATION

The *American Malacological Bulletin* serves as an outlet for reporting notable contributions in malacological research. Manuscripts concerning any aspect of original, unpublished research, important short reports, and detailed reviews dealing with molluscs will be considered for publication.

Each original manuscript and accompanying illustrations must be submitted with two additional copies for review purposes. Text must be typed on one side of 8-1/2 x 11 inch bond paper, double-spaced, and all pages numbered consecutively with numbers appearing in the upper right hand corner of each page. Leave ample margins on all sides.

Form of the manuscript should follow that outlined in the *Council of Biology Editors Style Manual* (sixth edition, 1994). This can be purchased from the CBE, 11 S. LaSalle Street, Suite 1400, Chicago, IL 60603, U.S.A.

Text, when appropriate, should be arranged in sections as follows:

1. Cover page with title, author(s) and address(es), and suggested running title of no more than 50 characters and spaces. Authors should also supply five key words, placed at the base of this page, for indexing purposes.
2. Abstract (less than 5% of manuscript length)
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6. Figure captions

All binomens must include the author attributed to that taxon the first time the name appears in the manuscript [e.g. *Crassostrea virginica* (Gmelin)]. This includes non-molluscan taxa. The full generic name along with specific epithet should be written out the first time that taxon is referred to in each paragragh. The generic name can be abbreviated in the remainder of the paragraph as follows: C. *virginica.*

References should be cited within text as follows: Hillis (1989) or (Hillis, 1989). Dual authorship should be cited as follows: Yonge and Thompson (1976) or (Yonge and Thompson, 1976). Multiple authors of a single article should be cited as follows: Beattie *et al.* (1980) or (Beattie *et al.,* 1980).

In the literature cited section of the manuscript references must also be typed double spaced. All authors must be fully identified, listed alphabetically and journal titles must be unabbreviated. Citations should appear as follows:

Beattie, J. H, K. K. Chew, and W. K. Hershberger. 1980. Differential survival of selected strains of Pacific oysters *(Crassostrea gigas)* during summer mortality. *Proceedings of the National Shellfisheries Association* 70(2):184-189.

Hillis, D. M. 1989. Genetic consequences of partial self fertilization on population of *Liguus fasciatus* (Mollusca: Pulmonata: Bulimulidae). *American Malacological Bulletin* 7(1):7-12.

Seed, R. 1980. Shell growth and form in the Bivalvia. *In: Skeletal Growth of Aquatic Organisms,* D. C. Rhoads and R. A. Lutz, eds. pp. 23-67. Plenum Press, New York.

Yonge, C. M. and T. E. Thompson. 1976. *Living Marine Molluscs.* William Collins Son & Co., Ltd., London. 288 pp.

Illustrations should be clearly detailed and readily reproducible. All line drawings should be in black, high quality ink. Photographs must be on glossy, high contrast paper. All diagrams must be numbered in the lower right hand corners and adequately labeled with sufficiently large labels to prevent obscurance with reduction by one half. Magnification bars must appear on the figure, or the caption must read Horizontal field width = xmm or xμm. All measurements must be in metric units. All illustrations submitted for publication must be fully cropped, mounted on a firm white backing ready for reproduction, and have author's name, paper title, and figure number on the back. All figures in plates must be nearly contiguous. Additional figures submitted for review purposes must be of high quality reproduction. Xerographic reproduction of photomicrographs or detailed photographs will not be acceptablefor review. Abbreviations used in figures should occur in the figure caption. Indicate in text margins the appropriate location in which figures should appear. Color illustrations can be included at extra cost to the author. Original illustrations will be returned to author if requested.

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Final submission of accepted, revised manuscripts should include two typed copies of the text, tables, etc. and an additional copy in electronic form on 3.5" diskette. The electronic version should be readable as **non-formatted** ASCII files.

New Taxa. The *Bulletin* welcomes complete descriptions of new molluscan taxa. Establishment of new taxa must conform with the International Code of Zoological Nomenclature (1985). Descriptions of new species-level taxa must include the following information in the order as given: higher taxon designation as needed for clarity; family name with author and date; generic name with author and date; *Genus species* author sp. *nov.* followed by numeration of all figures and tables; complete synonymy (if any); listing of type material with holotype and any other type material clearly designated along with complete museum catalogue or accession information; listing of all additional non-type material also with full museum deposition information; type locality; diagnosis and full description of material done in telegraphic style including measurements and zoogeographic distribution as necessary; discussion; etymology. Descriptions of new supraspecific taxa should include type species (for new genus) or type genus (for new family), diagnosis and full description done in telegraphic style, and list of included taxa.

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Ecological notes and patterns of dispersal in the recently introduced mussel, *Perna perna* (Linné, 1758), in the Gulf of Mexico. **DAVID W. HICKS** and **JOHN W. TUNNELL, JR.** 203

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